



Post-fire morel (*Morchella*) mushroom abundance, spatial structure, and harvest sustainability



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ARTICLE INFO

Article history:

Received 18 April 2016

Received in revised form 20 June 2016

Accepted 21 June 2016

Available online 27 June 2016

Keywords:

Mixed-severity fire

Morchella

Non-timber forest products

Rim Fire

Sierra Nevada

Wildcrafting

Yosemite Forest Dynamics Plot

Yosemite National Park

ABSTRACT

Morel mushrooms are globally distributed, socially and economically important reproductive structures produced by fungi of the genus *Morchella*. Morels are highly prized edible mushrooms and significant harvests are collected throughout their range, especially in the first year after fire, when some morel species fruit prolifically. Few studies have quantified post-fire morel mushroom abundance, despite their widespread human use. The purpose of this study is to provide the first ever estimate of post-fire morel mushroom abundance in Sierra Nevada mixed-conifer forest. Specifically, we estimate the abundance and spatial variability of morel mushrooms across an intensively mapped and measured forest research site during the first growing season following fire.

We conducted this study in the Yosemite Forest Dynamics Plot, a long-term forest research installation located in old-growth mixed-conifer forest of Yosemite National Park, California, USA. We surveyed for morel mushrooms in $n = 1119$ contiguous circular 3.14 m^2 plots arranged along 2240 m of permanently marked, georeferenced transects. We characterized the spatial correlation of morel plots using k category (multicolor) join count statistics. We analyzed spatial correlations at interplot distances up to 9.0 m.

There were 595 morel mushrooms in the 1119 plots we measured. Mushrooms occurred in 17.8% of plots. We estimated a mean standing crop of $1693 \text{ morels ha}^{-1}$ ($\text{SE} = 155.4 \text{ morels ha}^{-1}$). Morel-occupied plots were strongly and significantly spatially autocorrelated. Most of the spatial correlation among morel-occupied plots was apparent at scales up to 7.0 m, and was strongest at scales $<3.0 \text{ m}$.

This study is one of only four that provide unbiased estimates of post-fire morel abundance. Our morel abundance estimates are generally consistent with prior work in high-latitude North American conifer forests. The strong spatial autocorrelation of morel-occupied microsites at scales $<7 \text{ m}$ indicates that key factors controlling post-fire morel productivity are heterogeneous at small spatial scales. We propose a simple conceptual model to explain this spatial structure that includes spatial variability of pre-fire *Morchella* colonies; pre-fire vegetation community and fuelbed; fire behavior, intensity, and effects; and soil moisture and temperature. Relatively liberal harvest limits for recreational and subsistence harvesters appear appropriate and sustainable, at least for coniferous forests in the first year following fire. However, intensive commercial harvest, in jurisdictions where it is allowed, may warrant monitoring to assess potential impacts to long-term morel productivity, conflict with recreational harvesters, and non-target effects.

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1. Introduction

Morel mushrooms are globally distributed, socially and economically important reproductive structures (ascmata) produced

by fungi of the genus *Morchella* (Pilz et al., 2007; Matočec et al., 2014). Morels are highly prized edible mushrooms (Pilz et al., 2007), and significant recreational, subsistence, and commercial harvests are collected throughout their range (Schlosser and Blatner, 1993; Anderson et al., 2002; De Roman and Boa, 2004; McFarlane et al., 2005; Pérez-Moreno et al., 2008; Keefer et al., 2010). Some morel species reproduce prolifically in the first year

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following forest fires (Sturgis, 1905; Apfelbaum et al., 1984; Duchesne and Weber, 1993). Morel species that respond in this manner to fire are termed phoenicoid (Carpenter and Trappe, 1985) or pyrophilic (Greene et al., 2010); for clarity and simplicity we use the familiar non-technical term “burn morels.” The majority of the commercial harvest in western North America comprises burn morels collected in the first year following forest fires (Obst and Brown, 2000; McLain et al., 2005; Wurtz et al., 2005; Pilz et al., 2007). In California, members of several Native American tribes historically collected burn morels for food, and some tribal members continue to collect post-fire morels today (Anderson and Lake, 2013). Native Americans were aware of increased morel production following wildfires, and there is evidence that some tribes historically used fire to manage morel crops (Anderson and Lake, 2013). Given their widespread collection for human use, morels are a high priority for ecological research and monitoring to support their sustainable management and conservation (Parks and Schmitt, 1997; Pilz and Molina, 2002; Wurtz et al., 2005; Keefer et al., 2010).

Morels have complex life cycles and ecologies that are not yet completely understood for many individual species of *Morchella*. Volk and Leonard (1990) proposed a complete morel life cycle by studying yellow morels (Esculenta clade). Following germination of spores released from ascumata, homokaryotic mycelia grow and may either form resting structures known as sclerotia, or fuse with other compatible mycelia to produce heterokaryotic cells that may then produce sclerotia. Sclerotia are masses of dense, interwoven hyphae that store nutrients and are resistant to cold and desiccation (Pilz et al., 2007). Depending on conditions, sclerotia formed from either mycelial phase may go on to eventually form new ascumata, thereby completing the life cycle, or re-form mycelia. Additionally, a mitospore stage may occur, resulting in asexual reproductive structures known as conidiophores. These mitospore forms have been described for some species of black morels (Elata clade) in western North America, but their role in the overall life cycle is not clear (Carris et al., 2015).

Ecological relationships of some morel species have been inferred through observation of fruiting patterns or directly observed through experimentation. *Morchella rufobrunnea*, which has been identified as a basal species in the evolution of the genus (Du et al., 2012), has consistently been observed in landscaped and other disturbed areas, and has been successfully cultivated (Kuo, 2008). This suggests a saprotrophic role for this species and therefore a saprotrophic ancestry for the entire genus. Many other morel species reliably associate with particular tree species, a trait frequently exploited by mushroom hunters (Pilz et al., 2007). Dahlstrom et al. (2000) demonstrated mycorrhizal associations between black morels (two species of the Elata clade) and members of Pinaceae native to western North America. Baynes et al. (2012) found that several species of black morels are capable of endophytic relationships with grasses as well. It is possible that morels are variously saprotrophic and mycorrhizal at different stages of their life cycle (Pilz et al., 2007).

Mushroom hunters often distinguish between “natural” black morels that fruit in the absence of fire, and burn morels found in great abundance in forests after a fire. While ascumata formation of some *Morchella* species appears to be triggered solely by spring temperatures and precipitation (Buscot, 1989; Mihail et al., 2007), other species require an additional forest disturbance, such as fire, insect outbreaks, logging or wind storms (Pilz et al., 2004; McFarlane et al., 2005; Wurtz et al., 2005). Several mechanisms have been proposed for prolific mushroom production following tree death and disturbance events (reviewed and synthesized in Pilz et al., 2007), including loss of carbohydrate supply, changes in soil pH and chemistry (Winder, 2006), release from competition with other soil microorganisms, and flushes of available nutrients.

Greene et al. (2010) added to this list, proposing that forest fires remove deep duff accumulations from the forest floor in boreal and montane forests, eliminating a physical barrier to ascumata growth. In any case, Pilz et al. (2007) emphasize that the mechanisms promoting large crops of burn morels are an ecological mystery; it remains unsolved in the decade since Pilz et al. (2007) published their synthesis.

Morels are managed for recreational and commercial harvest throughout the fire-prone conifer forests of the western United States (Parks and Schmitt, 1997; McLain et al., 2005; Wurtz et al., 2005), but the peer-reviewed literature provides few data quantifying morel abundance or production in this region, with only one study published from sites in Oregon (Pilz et al., 2004), and another from sites in Alaska (Wurtz et al., 2005). New data on post-fire morel abundance and productivity will help inform management and harvest regulation, and adaptive management thereof (Keefer et al., 2010). Currently, morel collection in the western US is guided by highly idiosyncratic place-based rules and permitting systems (Wurtz et al., 2005). For example, some western US National Parks completely ban mushroom collection (e.g., North Cascades National Park and Glacier National Park) while others, such as Yosemite National Park, allow modest recreational collection but no commercial harvest (Yosemite National Park, 2015). Many US National Forests allow personal recreational and subsistence morel harvest with few or no regulations, but require commercial harvesters to obtain permits specific to each forest (McLain et al., 2005). Evaluation of the sustainability of these regulations requires scientifically credible estimates of morel abundance and productivity.

The purpose of this study is to provide the first ever estimate of post-fire morel mushroom abundance in Sierra Nevada mixed-conifer forest, with the aim of informing the management and conservation of this socially and economically important genus. Specifically, we seek to estimate the abundance and spatial variability of morel mushrooms across an intensively mapped and measured forest research site during the first growing season following fire. We hypothesize that morel-occupied sampling units will be highly spatially autocorrelated, because previous work provided preliminary evidence that post-fire morel production varies among microhabitats and burn severities at small scales within forest stands (Apfelbaum et al., 1984; Duchesne and Weber, 1993; Obst and Brown, 2000; Greene et al., 2010; Masaphy and Zabari, 2013). A secondary objective is to evaluate the sustainability of current Yosemite National Park morel collection regulations and interpret our results with respect to potential adaptive management actions. Finally, we place our results in the context provided by the global literature, and from this context develop generalizable management recommendations to support sustainable harvest and conservation of burn morels.

2. Methods

This study restricted identification of samples to the genus level due to the difficulty in identifying all potential species. This level of taxonomic resolution is appropriate given that harvest, management, and regulatory enforcement all occur at the genus level.

2.1. Study taxa

While true morels (genus *Morchella*, order Pezizales, phylum Ascomycota) have long been popular edible fungi, their global taxonomy has only recently begun to receive rigorous treatment (Pilz et al., 2007). The new techniques of molecular-based phylogenetics have allowed a significant revision of species concepts within the genus, which we briefly describe here in order to introduce the

taxa most likely to occur in the immediate post-fire environment in montane forests of western North America.

The traditional division of the genus into morphologically-distinct groups of yellow and black morels has been upheld (the Esculenta and Elata clades, respectively). However, molecular analysis has identified a large number of distinct species within each clade. Species distributions appear to be regional or continental more so than global, although there may be cases of accidental anthropogenic introduction outside their native ranges or natural long-distance dispersal (O'Donnell et al., 2011; Du et al., 2012).

The conifer-dominated montane forests across western North America, including the Sierra Nevada, likely share a similar species assemblage of morels. These *Morchella* species are mainly within the Elata clade of black morels and while some are identifiable from macroscopic or microscopic characteristics, others are cryptic species requiring molecular analysis to positively identify.

The western North American species clearly associated with wildfire are *Morchella eximia* (Richard et al., 2015, treated as *Morchella septimelata* in Kuo et al., 2012), *Morchella exuberans* (Richard et al., 2015, treated as *Morchella capitata* in Kuo et al., 2012), *Morchella sextelata* (Kuo et al., 2012), and *Morchella tomentosa* (Kuo, 2008). Only *M. tomentosa* is macroscopically distinguishable from the other burn morels by having densely tomentose ridges and stipe when young. The macroscopic identification of some burn morels by the colors green and pink (Pilz et al., 2004) has been shown to not correlate with molecular-based species concepts (Kuo et al., 2012). *Morchella brunnea* (Kuo et al., 2012), *Morchella snyderi* (Kuo et al., 2012), the mountain blond *Morchella tridentina* (Richard et al., 2015, treated as *Morchella frustrata* in Kuo et al., 2012), and the unnamed species labeled “Mel-8” (O'Donnell et al., 2011; Kuo et al., 2012) have been found in forests in western North America, but their relationship to fire, if any, is not clear. Two more species, *Morchella americana* (Richard et al., 2015, treated as *Morchella esculentoides* in Kuo et al., 2012) and *Morchella populiphila* (Kuo et al., 2012), are found in association with hardwoods (particularly *Populus*) in western North America and so are not likely to be represented in collections outside riparian habitats in the Sierra Nevada. Given the limited geographic density of molecular sampling up to this point, the precise ranges of species are still unclear and the discovery of additional cryptic species remains a possibility.

2.2. Study area

We conducted this study in the Yosemite Forest Dynamics Plot (YFDP). The YFDP is a long-term, 25.6 ha forest research installation located in old-growth (oldest trees > 500 yr) *Abies concolor*/*Pinus lambertiana* (white fir/sugar pine) mixed-conifer forest of Yosemite National Park between 1774 m and 1911 m elevation (Lutz et al., 2012, 2013; Keeler-Wolf et al., 2012; Fig. 1). Within the YFDP, all trees ≥ 1 cm diameter at breast height (dbh) have been individually measured, mapped, and tagged. Dominant tree species in 2010 (the first complete census) were *A. concolor* (956 stems ha^{-1} and 29.2 $\text{m}^2 \text{ha}^{-1}$), *P. lambertiana* (186 stems ha^{-1} and 28.75 $\text{m}^2 \text{ha}^{-1}$), *Cornus nuttallii* (93 stems ha^{-1} and 0.26 $\text{m}^2 \text{ha}^{-1}$), *Calocedrus decurrens* (62 stems ha^{-1} and 4.78 $\text{m}^2 \text{ha}^{-1}$), and *Quercus kelloggii* (43.3 stems ha^{-1} and 1.12 $\text{m}^2 \text{ha}^{-1}$).

The historical fire regime of the YFDP was characterized by low- and moderate-severity surface fires, occurring with a mean return interval of 29.5 years (Barth et al., 2015). Lightning-ignited spot fires have occurred since 1900, but the YFDP and the surrounding landscape have been largely fire-excluded since the last widespread fire event in 1899 (Scholl and Taylor, 2010), with concomitant accumulation of surface fuels (Gabrielson et al., 2012; Lutz et al., 2012) and densification of the forest canopy (Barth et al., 2015).

The YFDP burned on September 1st and 2nd, 2013 in a management-ignited fire set to control the spread of the Rim Fire (Kane et al., 2015). After ignition, which occurred 1 km from the plot, the fire was allowed to burn without further intervention. The fire backed through the western half of the plot at night on September 1, 2013, and the eastern half was burned the following day as the fire burned upslope. Smoldering combustion lasted for days with some areas smoldering for weeks through the early snowfalls of October 2013. Post-fire mortality of the dominant tree species (percent of stems ≥ 1 cm dbh) as of May 2014 was 73% for *A. concolor*, 64% for *P. lambertiana*, 76% for *C. nuttallii*, 64% for *C. decurrens*, and 63% for *Q. kelloggii*, with most mortality concentrated in stems <30 cm dbh. The Rim Fire reduced surface fuels in the YFDP >90%. Pre-fire litter and duff levels were 63.9 and 188.8 Mg ha^{-1} , respectively, decreasing to 3.22 and 13.1 Mg ha^{-1} post-fire. Pre-fire woody surface fuels in the 1-h, 10-h, 100-h, and 1000-h fuel classes were 0.62, 3.00, 9.04, and 69.1 Mg ha^{-1} , respectively, decreasing to 0.06, 0.42, 0.35, and 26.8 Mg ha^{-1} . These post-fire estimates exclude surface fuels added via post-fire deposition.

2.3. Field measurements

Research staff made daily observations of the local morel crop (and collections for personal use) from early May through the end of July during the 2014 field season. Based on these continuous observations our sampling occurred shortly after the peak of morel production. On May 18–25, 2014, we surveyed for morel mushrooms in $n = 1119$ contiguous circular plots of 1 m radius (3.14 m^2) plots arranged along 2240 m of permanently marked transects (Fig. 1). Transects are marked every 20 m with georeferenced stainless steel rods, the locations of which were surveyed with Total Stations to a pre-fire positional accuracy of 5 cm (Lutz et al., 2012). We recorded the absence or abundance (count) of morels in each plot, and also estimated the percentage surface area burned of each plot. All morels in each sample plot, including old, dehydrated, or decomposing ascomata unsuitable for harvest and consumption, were counted, ensuring our sample encompassed all past production during the 2014 season.

Members of our research team collected a total of 42 individual pints (473.2 mL) of whole morels from the area immediately surrounding the YFDP on three consecutive days, May 25–27, 2014, in accordance with Yosemite Park regulations, which allow each visitor to collect a single pint of morel mushrooms per day (Yosemite National Park, 2015). In the camp kitchen, we recorded the number of individual entire morel mushrooms in each pint then pooled the morels in a common container. After pooling morels, we randomly drew individual mushrooms, sliced them in half longitudinally, and deposited both pieces of the halved mushrooms in a pint container, recording the number of halved mushrooms in each full pint. We did this so that our count to volume ratios would be relevant to USDA National Forest Service lands and other land management agencies, many of which require recreational morel harvesters to halve mushrooms as they are collected so they are not marketable to commercial buyers.

2.4. Analysis

We characterized the spatial correlation of morel plots using k category (multicolor) join count statistics (Cliff and Ord, 1973, 1981). Join count statistics are used to determine if spatial associations among neighboring sampling units with categorical attributes deviate from that expected under complete spatial randomness (Fortin and Dale, 2005). We first reduced our morel count data to four density categories: unoccupied (zero morels per plot), low (1 morel per plot), medium (2–3 morels per plot), or high (≥ 4 morels

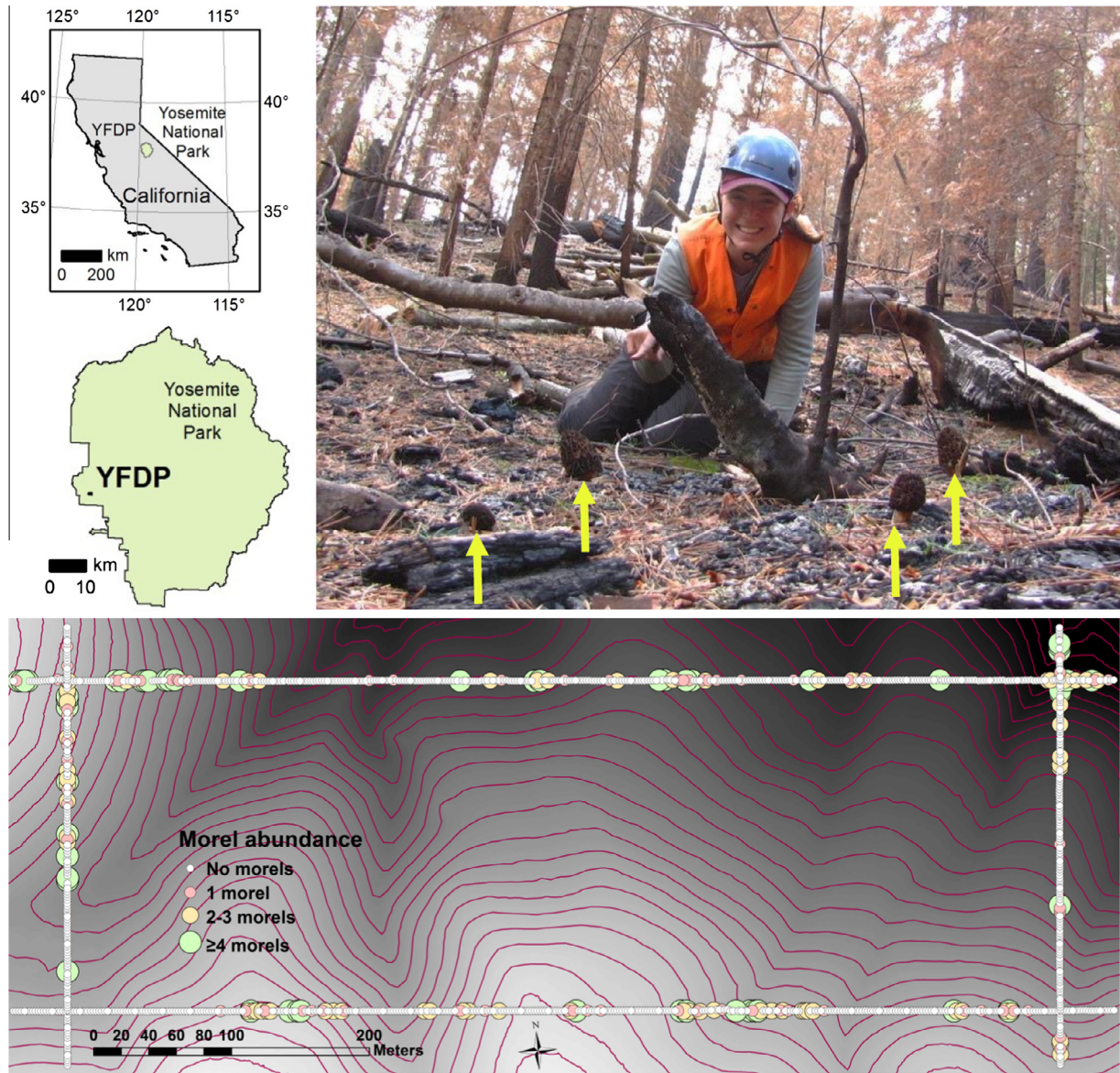


Fig. 1. Location of the Yosemite Forest Dynamics Plot (YFDP; upper and middle left), representative post-fire conditions in May 2014 (upper right), and locations of morel sampling plots along systematically arrayed transects within the YFDP (bottom). The light-to-dark grayscale gradient shows the elevation gradient from higher (light gray) to lower (dark gray) elevations within the YFDP. Yellow arrows in the upper right panel indicate morel mushrooms. May 2014 photo by S. Hiebert. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

per plot). We then constructed neighbor lists using Euclidian distance between plot centers. We analyzed nearest neighbor plots, defining neighbors as plots located <3.0 m apart (plot center to plot center distance). We then developed neighbor lists for lag 2 (plots spaced 3.0–5.0 m apart), lag 3 (plots spaced 5.0–7.0 m apart), and lag 4 (plots spaced 7.0–9.0 m apart) plots. This let us investigate if and how the spatial correlation structure changed with distance between plots. Join count analyses were conducted with the statistical program R version 3.2.4 (R Core Team, 2016) using the 'spdep' package (Bivand, 2015). We used the spatial weighting method of Kelejian and Prucha (2010), but the results were qualitatively similar for all of the weighting schemes available in the spdep package. To control for multiple tests (ten tests at each of four neighbor distances) we used Bonferroni correction with $\alpha = 0.00125$. We considered P -values ≤ 0.00125 as indicative of statistically significant spatial correlation, and $0.01 \geq P$ -values > 0.00125 as evidence of marginal significance.

To provide landscape context for our morel production estimates we calculated the annual area burned in forests belonging to the white fir superassociation (Keeler-Wolf et al., 2012) within the Yosemite National Park. We used the park fire atlas (fire record keeping began in 1930) and the 1997 park vegetation map to calculate total area burned since 1930 and annual area burned from 1984 to 2014 for the white fir superassociation.

3. Results

There were 595 morel mushrooms in the 1119 plots we measured (Fig. 1). Mushrooms occurred in 17.8% of plots, the remaining 82.2% of plots did not contain morels. The maximum count of morels within a single 3.14 m² plot was 16 individuals, which occurred once (Fig. 2, left panel). We estimated a mean standing crop of 1693 morels ha⁻¹ (SE = 155.4 morels ha⁻¹), with a 95% confidence

interval of 1388–1998 morels ha^{-1} . Morels did not occur in plots in which <50% of the surface was burned; the overwhelming majority of morel-occupied plots were 100% burned (Fig. 3, right panel).

Morel-occupied plots were strongly and significantly spatially autocorrelated, as were plots unoccupied by morels (Table 1). Adjacent plots (lag 1, plot centers <3.0 m apart) categorized as unoccupied, medium, or high morel occupancy (Fig. 1) were more likely to occur next to plots of the same type than expected under spatial randomness; low-low adjacencies were not different from spatial randomness (Tables 1 and A1). Unoccupied (zero morels) plots were less likely to occur adjacent to occupied plots (for low, medium, or high morel abundance categories) than expected under spatial randomness (Tables 1 and A1). These general relationships held, but were weaker (Table 1), for lag 2 neighbors (plots spaced 3.0–5.0 m apart; Table A2), and a few persisted at a lag 3 (plots spaced 5.0–7.0 m apart; Table A3). At lag 4 (plots spaced 7.0–9.0 m apart), most of the spatial autocorrelation that was significant at shorter lag distances became either marginally significant or non-significant (Tables 1 and A4). For example, the significant positive high-high autocorrelation at lags 1, 2, and 3 became non-significant at lag 4: i.e., high plots are not more likely to be neighbors of other high plots than expected by chance at distances >7 m (Table 1). Most of the spatial correlation among morel-occupied plots is apparent at scales up to 7.0 m, and is strongest at scales <3.0 m. In other words, morel-occupied plots are more likely to occur within about 7.0 m of each other than would be expected if morels were randomly distributed throughout the study area.

Based on $n = 42$ pints of harvested morels, mean morel bulk density was 17.4 morels pint^{-1} (SD 5.3 morels pint^{-1}). For halved morels ($n = 37$ pints) we estimated a mean bulk density of 19.2 morels pint^{-1} (SD 5.2 morels pint^{-1}). Combining these mushroom bulk densities with our estimate of mushroom abundance (1963 morels ha^{-1}) and the current Yosemite National Park allowable harvest of 1 pint day^{-1} yields a total harvestable crop of 97 person harvest days ha^{-1} for entire mushrooms and 88 person harvest days ha^{-1} for halved mushrooms (Fig. 3).

Within the boundaries of Yosemite National Park, forests dominated by the white fir superassociation (Keeler-Wolf et al., 2012), the forest type in which the YFDP is located, total 24,197 ha (242 km^2 ; 8% of park area). Of this total, 21,020 ha have burned at least once since the advent of fire record keeping in 1930, with area burned totaling 19,835 ha during 1984–2014. This translates to an annual mean area burned of 640 ha (range: 15.5–7564.3 ha) in the white fir superassociation during the period 1984–2014. Applying our per hectare morel productivity estimates, burned white fir forests in Yosemite National Park produce a mean crop of

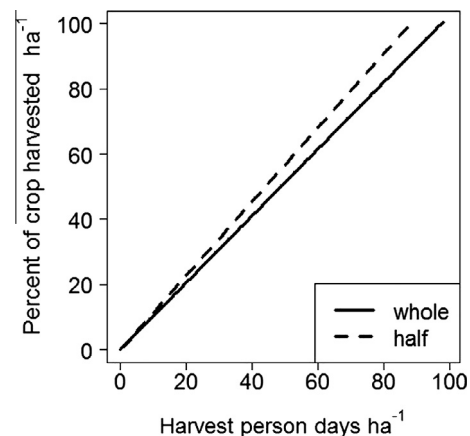


Fig. 3. Harvest depletion curves for the 2014 burn morel crop in Yosemite National Park expressed on a per hectare basis. Curves are based on an allowable morel harvest of 1 pint $\text{person}^{-1} \text{day}^{-1}$ (Yosemite National Park, 2015), mean morel abundance of 1693 morels ha^{-1} , and a mean morel bulk density of 17.4 morels pint^{-1} for entire morels, and 19.2 morels pint^{-1} for halved morels.

1,083,520 morels yr^{-1} (range: 26,226–12,806,320 morels yr^{-1}), or 62,271 potential harvest person days yr^{-1} (range: 1507–735,995 harvest person days yr^{-1}).

4. Discussion

Our estimate of post-fire morel abundance—the first of which we are aware for Sierra Nevada mixed-conifer forest—is generally consistent with the available data quantifying post-fire morel abundance in other North American conifer forests (Table 2). One key consideration when comparing our results to those summarized in Table 2 is that we only sampled during an one-week period, while morel production in the first season after fire can last for several weeks or even months (Obst and Brown, 2000; Pilz et al., 2004, 2007). Thus, our estimate of post-fire morel abundance in the YFDP likely underestimates total 2014 production at our study site, but only modestly so—we observed only incidental morel production in the eight weeks following our sampling campaign. Additionally, our landscape-scale estimates are only for burned forests of the white fir superassociation and therefore severely underestimate the total annual morel productivity in Yosemite National Park, as morels are not restricted to the white fir forests, nor are they restricted to burned areas (Pilz et al., 2007).

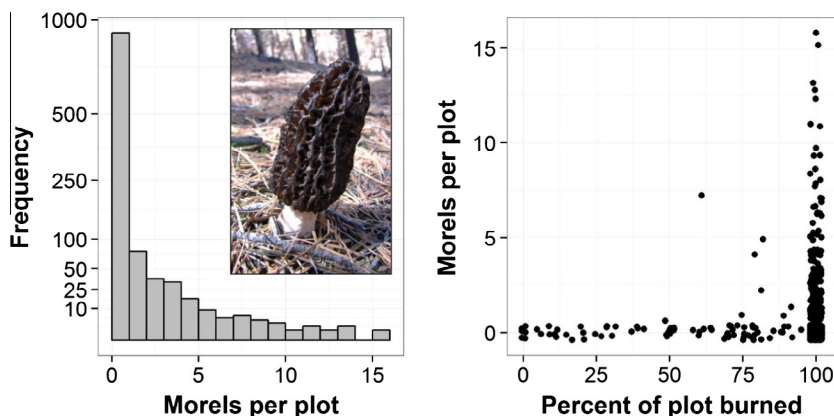


Fig. 2. Frequency of morel counts within 3.14 m^2 circular plots within the Yosemite Forest Dynamics Plot (left) and relationship of morel abundance to proportion of 3.14 m^2 plot surface burned (right; results have been “jittered” by adding small random variation in the x and y dimensions to avoid plotting over identical data values). May 2014 inset photo by A.J. Larson.

Table 1

Summary results (Z scores and P-values) of multicolor join count tests conducted at different lag distances between morel sampling plots in the Yosemite Forest Dynamics Plot. To control for multiple tests (ten tests at each of four neighbor distances) we used Bonferroni correction with $\alpha = 0.00125$. We considered P-values ≤ 0.00125 as indicative of statistically significant spatial correlation, and $0.01 \geq P$ -values > 0.00125 as evidence of marginal significance. Significant values shown in bold, marginally significant values underlined. Full results for each lag distance are presented in Tables A1–A4.

Neighbor type	Lag 1: <3 m		Lag 2: 3–5 m		Lag 3: 5–7 m		Lag 4: 7–9 m	
	Z	P	Z	P	Z	P	Z	P
Zero – Zero	9.960	<0.001	5.237	<0.001	4.318	<0.001	2.863	<u>0.002</u>
Low – Low	1.285	0.099	3.036	<0.001	0.196	0.422	0.183	0.428
Medium – Medium	2.895	<u>0.002</u>	3.794	<0.001	2.162	0.015	5.550	<0.001
High – High	6.525	<0.001	5.714	<0.001	2.272	<u>0.012</u>	0.303	0.381
Low – Zero	–5.731	<0.001	–3.229	<0.001	–2.912	<u>0.002</u>	–2.740	<u>0.003</u>
Medium – Zero	–6.893	<0.001	–3.426	<0.001	–4.206	<0.001	–3.679	<0.001
Medium – Low	5.252	<0.001	0.367	0.357	4.523	<0.001	2.845	<u>0.002</u>
High – Zero	–10.002	<0.001	–6.093	<0.001	–3.433	0.001	–1.377	0.084
High – Low	4.662	<0.001	2.187	<u>0.014</u>	2.043	0.021	2.772	<u>0.003</u>
High – Medium	4.731	<0.001	1.747	0.040	1.222	0.111	–0.376	0.353

Recognition of the diverse sampling approaches used in earlier studies (Table 2) is another important consideration when comparing our results to the literature. We used an unbiased, systematic sampling approach to estimate morel mushroom abundance, and therefore our results are most directly comparable to those of Pilz et al. (2004) and Wurtz et al. (2005), who also used systematic sampling, and Winder and Keefer (2008), who used randomly located sample plots. Others have used targeted sampling, such as Greene et al. (2010) who only sampled in areas of 100% tree mortality, which may explain why they estimated 14,900 morels ha^{-1} for a 2003 wildfire in Kootenay National Park, nearly double the 8062 morels ha^{-1} estimated for the same fire using randomly located plots (Winder and Keefer, 2008). The very high post-fire morel abundance reported by Duchesne and Weber (1993), 2860 kg ha^{-1} (Table 2), is likely the result of targeted sampling with 1 m^2 plots of the most productive microhabitats within their 0.21 ha study area. Pilz et al. (2007) estimated that the 2860 kg ha^{-1} reported by Duchesne and Weber (1993) was equivalent to about 148,000 morels ha^{-1} . Using the mean morel fresh mass of 15.4 g per morel reported by Obst and Brown (2000), we obtain another estimate of 186,000 morels ha^{-1} for Duchesne and Weber's (1993) study site. Scaling our most densely occupied sample plot (Fig. 2) to a per hectare basis yields an estimate of 50,930 morels ha^{-1} , and we observed more densely occupied microsites in the YFDP than were captured in our systematic sample (Fig. 4). Thus, at the microsite scale ($<10 \text{ m}^2$), the estimate of Duchesne and Weber (1993) is a biologically plausible upper bound of post-fire morel production (c.f. morel "hotspots" described by Obst and Brown, 2000), but we are very skeptical that such productivity would ever be validated across large areas with unbiased sampling. In general, it seems that typical 1st year post-fire morel abundance in conifer forests of North America (Table 2) averages around 1965 morels ha^{-1} , with a 95% confidence interval of 506–3423 morels ha^{-1} , based on our data and the unbiased samples reported by Pilz et al. (2004), Wurtz et al. (2005), and Winder and Keefer (2008).

Our spatial analyses (Table 1) demonstrated that morel-occupied plots (3.14 m^2) are spatially autocorrelated up to about 7 m, confirming the visually apparent spatial patchiness of morel distribution within the YFDP (Fig. 1) as a statistically significant pattern. The practical application of this result for morel collectors is that, if you find one mushroom, carefully search the area within about 3 m (10 feet) and continue to search out to about 7 m (23 feet), as additional mushrooms are likely to occur in this neighborhood.

The ecological question that follows from the results our spatial analysis is, "Why are morels distributed so patchily, and with such

small scales of spatial autocorrelation?" We propose a simple conceptual model (Fig. 5) encompassing a set of nested hypotheses that may explain the observed spatial patterns, which is intended to be tested with future work.

1. We begin with the proposition of Pilz et al. (2007) that burn morels fruit from mycelial colonies and sclerotia present in forest soils before, and surviving through, the fire event (see also Buscot, 1989). We further propose that these mycelial colonies are patchily distributed, likely at small spatial scales (Fig. 5). We consider this the first and key hypothesis to test in order to rule out post-fire dispersal and establishment of new *Morchella* colonies as explanatory of large post-fire morel crops and their patchy spatial distribution within burn perimeters.
2. We take as axiomatic that the pre-fire forest vegetation community (Larson and Churchill, 2012; Lutz et al., 2012, 2014) and the surface fuel bed (Keane et al., 2012; Gabrielson et al., 2012) are spatially heterogeneous at small scales (Fig. 5).
3. We further accept as given that fire behavior, intensity, and effects all vary at fine spatial scales (Fig. 5) in response to the heterogeneous fuel bed and the weather conditions under which the fire burns (Loudermilk et al., 2012), leading to patchiness in duff consumption (Greene et al., 2010), vegetation mortality (Belote et al., 2015), and fire-induced soil chemistry changes (Gundale et al., 2006). These fine scale differences in fire effects are correlated with variation in post-fire morel abundance (Greene et al., 2010; Masaphy and Zabari, 2013).
4. Small scale spatial variability of soil temperature and moisture introduce additional variation of morel productivity and fruiting season length (Buscot, 1989; Pilz et al., 2007).
5. Only when favorable conditions for these multiple limiting factors align in space are burn morels locally abundant. Because all of the limiting factors are variable at small scales (Fig. 5), spatially synchronous favorable conditions for morel mushroom production are rare, giving rise to the observed spatial autocorrelation at scales $<7 \text{ m}$ (Table 1).

4.1. Management implications

The mission of the US National Park Service is "to conserve scenery, natural and historic objects, and wildlife, and to provide for the enjoyment of those resources in a manner that will leave them unimpaired for the enjoyment of future generations" (Organic Act, 1916). Park managers therefore develop policies so that renewable resources, such as morels, may be enjoyed by visitors without being depleted over time.

Table 2

Estimates of morel mushroom productivity in the first year following forest fire taken from the literature.

Location	Fire year	Dominant tree species	Study area size, sampling approach, and plot size	Morel density (number ha ⁻¹)	Morel fresh weight (kg ha ⁻¹)	Source
Cook County, Minnesota, USA	1976	<i>Pinus banksiana</i> , <i>Picea mariana</i>	400 ha burn; sampling protocol not described but subjectively located 100 m ² plots implied	200–1500	–	Apfelbaum et al. (1984)
Eastern Ontario, Canada	1990	<i>Pinus banksiana</i> , <i>Pinus resinosa</i> , <i>Pinus strobus</i>	1 m × 1 m quadrats, subjectively located within 0.21 ha (30 m × 70 m) area	–	2860	Duchesne and Weber (1993)
Eastern Oregon, USA	1994	<i>Abies grandis</i> , <i>Pseudotsuga menziesii</i> , <i>Pinus contorta</i> , <i>Larix occidentalis</i> , <i>Pinus ponderosa</i>	Ten 2 m × 100 m strip plots, systematically spaced	2950 (600) 90% CI ± in parentheses	4.158 (1.819) 90% CI ± in parentheses	Pilz et al. (2004)
Eastern Oregon, USA	1994	<i>Abies grandis</i> , <i>Pseudotsuga menziesii</i> , <i>Pinus contorta</i> , <i>Larix occidentalis</i> , <i>Pinus ponderosa</i>	Ten 2 m × 100 m strip plots, systematically spaced	4350 (2342) 90% CI ± in parentheses	3.800 (2.608) 90% CI ± in parentheses	Pilz et al. (2004)
Eastern Oregon, USA	1994	<i>Abies grandis</i> , <i>Pseudotsuga menziesii</i> , <i>Pinus contorta</i> , <i>Larix occidentalis</i> , <i>Pinus ponderosa</i>	Ten 2 m × 100 m strip plots, systematically spaced	315 (202) 90% CI ± in parentheses	0.650 (0.470) 90% CI ± in parentheses	Pilz et al. (2004)
Northwest Territories, Canada	1998	<i>Picea glauca</i> , <i>Picea mariana</i> , <i>Betula papyrifera</i> , <i>Populus balsamifera</i>	Variable. Counts in 200 m transects; season-long observation of a 500 m ² plot; and estimates based on harvest rates per ha	354–2320	5.3–14.8	Obst and Brown (2000)
Fairbanks, Alaska, USA	2001	<i>Picea glauca</i> , <i>Alnus tenuifolia</i>	Ten 2 m × 100 m strip plots, systematically spaced	983	6.568	Wurtz et al. (2005)
Fairbanks, Alaska, USA	2002	<i>Picea mariana</i> , <i>Betula papyrifera</i> , <i>Populus tremuloides</i>	10, 2 m × 100 m strip plots, systematically spaced	10	0.009	Wurtz et al. (2005)
Fairbanks, Alaska, USA	2002	<i>Picea glauca</i> , <i>Picea mariana</i> , <i>Betula papyrifera</i>	Ten 2 m × 100 m strip plots, systematically spaced	225	1.061	Wurtz et al. (2005)
Southeast British Columbia, Canada	2003	<i>Pinus contorta</i> , <i>Abies lasiocarpa</i> , <i>Picea glauca</i> , <i>Tsuga heterophylla</i> , <i>Larix occidentalis</i> , <i>Populus balsamifera</i> , <i>Thuja plicata</i>	26, 50.5 m ² circular plots, randomly located	1132	–	Winder and Keefer (2008)
Southeast British Columbia, Canada	2003	<i>Pinus contorta</i> , <i>Pseudotsuga menziesii</i> , <i>Populus tremuloides</i> , <i>Larix occidentalis</i>	18, 50.5 m ² circular plots, randomly located	618	–	Winder and Keefer (2008)
Southeast British Columbia, Canada	2003	<i>Pinus contorta</i> , <i>Abies lasiocarpa</i> , <i>Picea glauca</i>	20, 50.5 m ² circular plots, randomly located	2237	–	Winder and Keefer (2008)
Southeast British Columbia, Canada	2003	<i>Abies lasiocarpa</i> , <i>Picea glauca</i>	10, 50.5 m ² circular plots, randomly located	1003	–	Winder and Keefer (2008)
Southeast British Columbia, Canada	2003	<i>Pinus contorta</i> , <i>Abies lasiocarpa</i> , <i>Picea glauca</i>	24, 50.5 m ² circular plots, randomly located	8062	–	Winder and Keefer (2008)
Kootenay National Park, British Columbia, Canada	2003	<i>Pinus contorta</i> , <i>Picea engelmannii</i> , <i>Abies lasiocarpa</i>	12, 1 m × 100 m plots, and four 1 m × 50 m plots, all subjectively located in areas of 100% tree mortality	14,900	–	Greene et al. (2010)
Northern Israel	2006	<i>Pinus halepensis</i>	3, 500 m ² plots in each of four microsite types. Plots haphazardly located within a 24 ha study area	Unburned: 92 Burned without salvage: 680 Burned with salvage: 3400 Burned with salvage and chipped slash: 8494	–	Masaphy and Zabari (2013)
Central Sierra Nevada, California, USA	2013	<i>Pinus lambertiana</i> , <i>Abies concolor</i> , <i>Calocedrus decurrens</i> , <i>Quercus kelloggii</i> , <i>Cornus nuttallii</i>	1119, 3.14 m ² circular plots, systematically arranged within a 25.6 ha study area	1693 95% CI: 1388–1998	–	This study

We consider the approach to managing recreational morel mushroom collection taken by Yosemite National Park managers as exemplary of conservative natural resource stewardship. In the absence of any scientific data quantifying morel production in Sierra Nevada conifer forests, park managers have set recreational harvest limits at the lowest practicable amount, 1 pint person⁻¹ day⁻¹ (Yosemite National Park, 2015). This very conservative harvest limit achieved

a difficult balance between facilitating positive visitor experiences, while still ensuring high likelihood of maintaining morel populations for future generations. Managing in an information-limited environment such as this is the ideal scenario for adaptive management as new information becomes available (Larson et al., 2013).

The current morel harvest regulations (Yosemite National Park, 2015) are exceptionally conservative relative to annual production



Fig. 4. A microsite supporting very high morel mushroom production within the Yosemite Forest Dynamics Plot. Such exceptionally high-producing microsites were not captured by our systematic sample. Targeted (i.e., biased) sampling of such highly productive microhabitats likely explains some of the very highest post-fire morel abundance estimates in the literature (Table 2). The knife is shown for scale and measures 11.0 cm long. May 2014 photo by A.J. Larson.

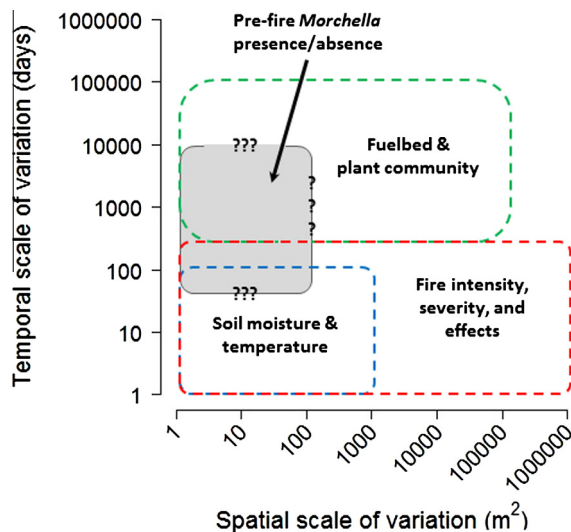


Fig. 5. Conceptual model illustrating the spatial and temporal variability of key factors thought to influence post-fire morel (*Morchella*) mushroom productivity (Mihail et al., 2007). We hypothesize that the strong spatial autocorrelation of morel-occupied sites at scales <7.0 m (Table 1) largely arises from the small scale variability (<10 m²) characteristic of several of the factors limiting morel mushroom production. The first control is hypothesized to be pre-fire presence or absence (and post-fire survival) of *Morchella* in the soil (Pilz et al., 2007); the spatial and temporal variability of which are uncertain. When suitable soil environmental conditions, burn severity, and vegetation community align in space with *Morchella* colonies there is potential for prolific localized mushroom production post-fire.

and likely recreation demand. Our data and analyses (Figs. 2 and 3), as well as our review of the global literature (Table 2), indicate that Yosemite National Park could responsibly liberalize recreational collection limits with very high likelihood of no impact to the resource. Because of the high density of morels in these *A. concolor* forests and the relatively short period of time post-fire during which the morels are in edible condition, it is almost impossible for recreational harvest to have an effect. For these reasons, and because harvest is not known to affect future production (Pilz et al., 2004; Egli et al., 2006), we infer that there is essentially no chance of negatively affecting morel populations or future mushroom production by modestly increasing the recreational harvest

limit. Similarly, inadvertent over collection by recreational harvesters would not appear to be a threat to the resource. Commercial harvest, on the other hand, could deplete a local area quickly, adversely impacting opportunities for other visitors to engage in recreational morel collection, and with unknown ecological consequences. We also suggest adding questions to regular visitor surveys about morel harvest, so managers have more information about this demographic and overall morel harvest rates.

Because the mission of the Park Service does not extend to economic extraction, and because of the potential to impair the experience of other visitors, commercial collection is thus a natural priority for regulatory enforcement at Yosemite National Park. Commercial morel harvest is certainly consistent with the mission of other land management agencies, such as the USDA Forest Service and the USDI Bureau of Land Management, and therefore an appropriate activity on lands managed by those agencies.

4.2. Conclusions

We draw three main conclusions with respect to the management and conservation of *Morchella* based on our data and our review of the global literature.

- Morel-occupied microsites are strongly spatially autocorrelated up to about 7 m, indicating that key factors controlling post-fire morel productivity are heterogeneous at small spatial scales. However, the relative importance of different factors influencing morel productivity remains largely unknown, highlighting an important role for additional research on the mechanisms controlling post-fire morel production. The conceptual model we propose (Fig. 5) can be used as a starting point for future investigations of *Morchella* productivity. We consider a rigorous test of the hypothesis of Pilz et al. (2007) that burn morels fruit from mycelial colonies and sclerotia present in forest soils before, and surviving through, the fire event as the first and key step to solving this problem.
- There is a strong need to conduct inventories of post-fire morel abundance using unbiased, statistically valid sampling designs, and to publish the results in the peer-reviewed literature. Astonishingly little has been published about the productivity of this socially and economically important genus (Table 2). This study is one of only four (Pilz et al., 2004; Wurtz et al.,

2005; Winder and Keefer, 2008) that provide unbiased estimates of post-fire morel abundance.

- Relatively liberal harvest limits (e.g. $\geq 4 \text{ L day}^{-1}$) for recreational and subsistence harvesters appear appropriate and sustainable, at least for coniferous forests in the first year following fire (Table 2). The magnitude of post-fire morel production overwhelms the any plausible level of recreational harvest (Obst and Brown, 2000). However, intensive commercial harvest may warrant monitoring to assess potential impacts to long-term morel productivity, conflicts with recreational harvesters, and potential non-target effects (Larson et al., 2013; Hutto and Belote, 2013).

Acknowledgements

Funding was provided by the National Park Service (Awards P14AC00122 and P14AC00197) and the Utah Agricultural Extension Station, Utah State University, which has designated this as journal paper number #8890. We thank Yosemite National Park for logistical assistance and the Yosemite Forest Dynamics Plot field crew members, individually acknowledged at <http://yfdp.org>. This work was performed under National Park Service research permits YOSE-2013-SCI-0012 and YOSE-2014-SCI-0005 for study YOSE-0051.

Appendix A

See Tables A1–A4.

Table A1

Join count statistics for lag 1 (0–3 m) neighbors. Significant values shown in bold, marginally significant values underlined.

Neighbor type	Join count statistic		Variance	Z	P
	Observed	Expected			
Zero – Zero	163.000	151.654	1.298	9.960	<0.001
Low – Low	1.600	1.050	0.183	1.285	0.099
Medium – Medium	2.000	0.866	0.153	2.895	<u>0.002</u>
High – High	2.400	0.476	0.087	6.525	<0.001
Low – Zero	19.000	25.413	1.252	−5.730	<0.001
Medium – Zero	15.800	23.103	1.122	−6.893	<0.001
Medium – Low	5.000	1.934	0.341	5.252	<0.001
High – Zero	8.200	17.162	0.803	−10.001	<0.001
High – Low	3.800	1.436	0.257	4.662	<0.001
High – Medium	3.600	1.306	0.235	4.731	<0.001

Table A2

Join count statistics for lag 2 (3–5 m) neighbors. Significant values shown in bold, marginally significant values underlined.

Neighbor type	Join count statistic		Variance	Z	P
	Observed	Expected			
Zero – Zero	135.833	129.532	1.447	5.237	<0.001
Low – Low	2.000	0.897	0.132	3.036	<0.001
Medium – Medium	2.000	0.74	0.11	3.794	<0.001
High – High	1.833	0.406	0.062	5.714	<0.001
Low – Zero	18.333	21.706	1.091	−3.229	<0.001
Medium – Zero	16.333	19.733	0.984	−3.426	<0.001
Medium – Low	1.833	1.652	0.245	0.367	0.357
High – Zero	9.500	14.659	0.717	−6.093	<0.001
High – Low	2.167	1.227	0.185	2.187	<u>0.014</u>
High – Medium	1.833	1.115	0.169	1.747	0.040

Table A3

Join count statistics for lag 3 (5–7 m) neighbors. Significant values shown in bold, marginally significant values underlined.

Neighbor type	Join count statistic		Variance	Z	P
	Observed	Expected			
Zero – Zero	120.286	114.793	1.618	4.318	<0.001
Low – Low	0.857	0.795	0.102	0.196	0.422
Medium – Medium	1.286	0.656	0.085	2.162	0.015
High – High	0.857	0.36	0.048	2.272	<u>0.012</u>
Low – Zero	16.286	19.236	1.026	−2.912	<u>0.002</u>
Medium – Zero	13.429	17.488	0.931	−4.206	<0.001
Medium – Low	3.429	1.464	0.189	4.523	<0.001
High – Zero	10.143	12.991	0.688	−3.433	<0.001
High – Low	1.857	1.087	0.142	2.043	0.021
High – Medium	1.429	0.988	0.13	1.222	0.111

Table A4

Join count statistics for lag 4 (7–9 m) neighbors. Significant values shown in bold, marginally significant values underlined.

Neighbor type	Join count statistic		Variance	Z	P
	Observed	Expected			
Zero – Zero	104.375	100.951	1.431	2.863	<u>0.002</u>
Low – Low	0.750	0.699	0.079	0.183	0.428
Medium – Medium	2.000	0.576	0.066	5.550	<0.001
High – High	0.375	0.317	0.037	0.303	0.381
Low – Zero	14.375	16.917	0.861	−2.740	<u>0.003</u>
Medium – Zero	12.125	15.379	0.782	−3.679	<0.001
Medium – Low	2.375	1.287	0.146	2.845	<u>0.002</u>
High – Zero	10.375	11.424	0.581	−1.377	0.084
High – Low	1.875	0.956	0.110	2.772	<u>0.003</u>
High – Medium	0.750	0.869	0.100	−0.376	0.353

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