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RESEARCH ARTICLE

Off-road Vehicle-Induced Substrate Vibrations Are Associated with Strong Declines in Ectomycorrhizal Mushroom Fruiting in Forest Ecosystems

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Abstract: We conducted a multi-year (2020-2024) control-impact field study in a pine forest of the Moscow Region to assess whether off-road vehicle activity affects the fruiting of two ecologically important ectomycorrhizal fungi, *Boletus edulis* and *Suillus luteus*. Substrate vibrations associated with vehicle passage were recorded and characterized by dominant energy in the low-frequency range. Over the study period, abundance in disturbed zones declined significantly relative to undisturbed control sites. By 2024, counts of *S. luteus* had decreased to approximately 22% of control levels, while *B. edulis* was nearly absent. Statistical modeling confirmed a highly significant negative association between anthropogenic disturbance and fruiting body abundance for both species, whereas interannual variation in July temperature and humidity showed no statistically significant effects. These results are consistent with the hypothesis that substrate-borne vibrations and/or associated indirect environmental stressors linked to off-road vehicle activity may reduce ectomycorrhizal fungal fruiting even in the absence of visible physical habitat damage.

Keywords: Boletus edulis, Suillus luteus, Ectomycorrhizal Fungi, Off-road Vehicle Disturbance, Substrate Vibrations, Forest Soil Ecology, Anthropogenic Impact, Fungal Fruiting Dynamics, Pine Forest Ecosystems, Environmental Noise Pollution

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Introduction

Soil ecosystems are increasingly recognized as subject to significant transformation through human-mediated disturbances [1]. Although the ecological impacts of direct disturbances, particularly chemical pollution and mechanical habitat destruction, have been well documented [2,3], indirect anthropogenic factors such as substrate vibrations have received considerably less attention in environmental impact assessments. This oversight persists despite increasing awareness of vibration-sensitive species that depend on specialized communication systems for critical life functions [4]. Notably, current conservation frameworks rarely consider how anthropogenic vibrations disrupt biological communication networks, even in soil ecosystems where such disturbances are both ecologically significant yet remain poorly quantified.

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Vibrational communication is evolutionarily older than airborne signal transmission. Most invertebrates use this form of communication [5-9]. Soil vibrations can travel long distances. These low-frequency signals help organisms gather important information [10,11]. Both small animals and complex vertebrates use this system. Examples include fish, amphibians, and even large mammals like elephants [12,13]. If we consider the process of vibration impact and their role in communication in an ecological context, it becomes obvious that in nature communication occurs not only between individuals of the same species, but in a group of several animals within the range of signal transmission [6-8]. That is, this process is multilateral, and individuals of different species, simultaneously located together in the same biotope, participate in it [4]. The communication scheme itself, according to some authors, has a complex network rather than a linear structure [4]. In this case, the signal can be used not by the one for whom it was intended, but, for example, by predators and parasites. Thus, the opinion that vibrational communication channels are a shorter-range form of communication compared to air channels is incorrect [14]. Some researchers believe that the first step to changing this perception is to obtain more data on the fact that vibrational signal transmission is one of the most common forms of animal communication and that signals are available to representatives of other species, including potential enemies [4]. At present, there is no doubt that this fundamental direction requires additional study.

Studies on the impact of vehicle emissions on the activity and diversity of soil communities in roadside areas are common [1]. For example, emissions from roadside vehicles have been shown to reduce species diversity over time, indicating the potential for decreased ecosystem functionality in these soils [1]. However, there are currently no studies specifically investigating the impact of soil fluctuations caused by motor vehicles on fungal communities. However, there is some indirect evidence suggesting the importance of this factor. For example, long-term grazing and driving livestock to pastures has been shown to negatively affect plant and fungal growth [3]. Reindeer grazing can lead to erosion, prevent the formation and recovery of vegetation, and contribute to changes in soil and vegetation cover due to grazing, trampling, and nutrient enrichment [2]. As a result, undisturbed ecosystems with high biodiversity and productivity can be replaced by secondary ecosystems with a poorer species composition and altered soil characteristics. In some studies, researchers have attempted to determine whether environmental fluctuations influence fungal growth and the formation of fruiting bodies [15].

While biological communication has been widely studied, the role of vibrational signals in ecosystems remains poorly understood. In particular, it remains unclear what is the role of anthropogenic substrate vibrations on natural biotopes subject to this load. Can such noises be a factor influencing biodiversity and sustainability of ecosystems at the same time, most fundamental ecological problems can be solved only on fairly large-scale objects. In this case, mushrooms are the best fit, in addition, they are easy to quantify during the formation of fruiting bodies. Interest in the influence of various anthropogenic pollution on the growth and fruiting of various types of mushrooms is due not only to the fundamental tasks of studying ecological processes, but also to their important role as wild plants included in the human diet.

This study aims to assess whether anthropogenic substrate vibrations from off-road vehicle activity influence the fruiting body production of *B. edulis* and *S. luteus* in forest ecosystems.

Material and methodology.

The source material for the work was collected in the field. Field data were collected in the Moscow Region, Stupino District (coordinates: 54.846457°N, 38.022712°E), within a pine-dominated mixed forest. Sampling was conducted from 2019 to 2024 during the mushroom fruiting seasons (summer to autumn). The accounting dates and the number of fruit bodies by day for both species are presented in the supporting materials.

Add- Site Design and Sampling Strategy

The study compared fungal abundance between off-road vehicle trails (unauthorized routes) and adjacent control plots with restricted access to vehicles. Both trail and control sites were located within the same forest habitat to control for environmental variables.

Habitat Description

The two transects (undisturbed and disturbed) were established in close proximity (<100 m apart) within a homogeneous *Pinus sylvestris*-dominated forest stand and remained spatially fixed throughout the study period (2020-2024). Vegetation structure and microhabitat characteristics were visually indistinguishable between plots.

The understory was sparse and species-poor, composed primarily of *Betula spp*., *Populus tremula*, and young *Pinus sylvestris*. Herbaceous cover was dominated by *Polygonatum officinale* and *Convallaria majalis*. The forest floor was covered either by a layer of pine needle litter or by ground vegetation including *Cladonia spp*. lichens, *Sphagnum* mosses, and ericaceous dwarf shrubs (*Vaccinium vitis-idaea* and *V. myrtillus*). Pine canopy closure was measured at 0.6 in both transects, consistent with the typical range (0.6-0.8) reported for the Oka River botanical-geographical region. Soil profiles were examined in both plots. Given their proximity and shared biotope, the profiles were nearly identical and classified as weakly developed podzolic (or sod-podzolic).

Target Species Justification

Two common and ecologically important mushroom species were selected: *Boletus edulis* (porcini) and *Suillus luteus* (slippery jack). These species often co-occur in similar habitats, have large and easily identifiable fruiting bodies, and are minimally affected by standard forestry activities such as sanitary logging. Fruiting typically occurs when average daily temperatures remain between 15-18°C, facilitating consistent seasonal monitoring. Fruit bodies are large and species identification is easy to make visually, making them convenient for pedestrian surveys. Under optimal conditions, fruiting in neighboring forests within the same habitat occurs synchronously, allowing for comparative studies. The sample size for each species was determined by the total count of fruiting bodies observed during the study period, with a daily average of approximately 90 (mean annual values are presented in the results section for each species).

This study comparing two transects: one in an anthropogenically disturbed site and one in an intact control site. Each transect measured 1 km in length and 50 m in width (Fig.1.). The sites were selected within the same natural topographic depression, delineated by low hills on both sides, to ensure comparable microclimatic conditions. Both sites are located within the buffer zone of a forest reproductive area, where regulations prohibit hunting and off-road vehicle traffic but permit pedestrian access and foraging of non-timber forest products (e.g., wild mushrooms). Site selection was informed by long-term observational data from local residents, which indicated that both areas have consistently supported high-density mushroom fruiting for decades, even during periods of low productivity in adjacent forests. All fungal fruiting bodies encountered along each transect were identified, and counted in situ at the end of each survey route.

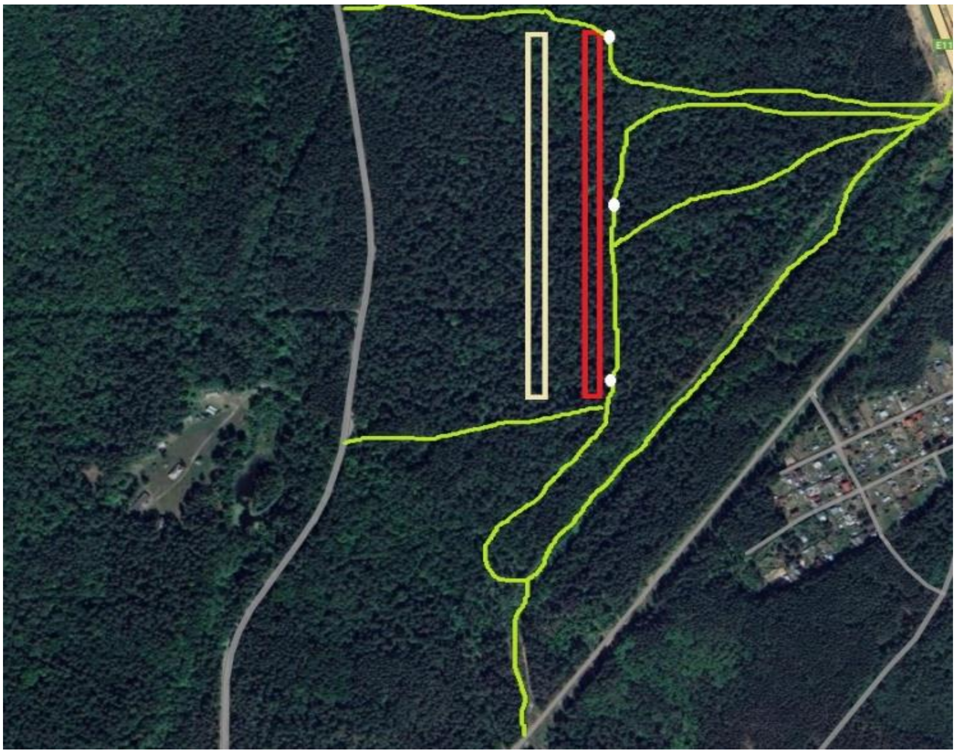

Fig. 1: Sampling design. The white rectangle indicates the control transect (no anthropogenic disturbance). The red rectangle marks the disturbed transect, adjacent to unauthorized off-road vehicle trails (yellow lines). White circles show approximate locations of substrate vibration recording points. Both transects are 1 km long and 50 m wide and are situated within the same forest biotope to ensure comparable environmental conditions

Meteorological data

Mean daily air temperature and relative humidity for July 2019-2024 were obtained from the official archive of the Kashira meteorological station (WMO ID 27627; 54.83°N, 38.15°E), located approximately 6.5 km from the study site. These observational data are provided by the Federal State Budgetary Institution “Russian Institute for Hydrometeorological Information - World Data Centre” (RIHMI-WDC) via the Unified State System for Environmental Monitoring (ESIMO; http://esimo.ru/). The same records are used by multiple public weather services (e.g., world-weather.ru) for regional forecasts and historical summaries in the Moscow region.

For comparison and reproducibility, we also evaluated the ERA5-Land reanalysis dataset (Copernicus Climate Data Store, https://cds.climate.copernicus.eu/). However, due to the coarse spatial resolution of reanalysis products (≈9 km grid), even ERA5-Land does not provide station-level data closer to our site than the Kashira observatory. Consequently, ERA5-derived values showed greater smoothing of local climatic variability and were deemed less representative. Although the station is not co-located with the transects, both study plots are situated only 100 m apart and share identical topography and vegetation cover. Thus, we assume that inter-annual weather variability, not absolute microclimatic differences, drives any potential climatic influence on fruiting.

Vibration Measurement and Analysis

Substrate-borne vibrations were measured using a portable laser Doppler vibrometer (Polytec PDV-100, Polytec GmbH, Germany), which enables non-contact, high-resolution recording of surface velocity (range: ±100 mm/s; resolution: <0.1 μm/s RMS). The instrument’s analog output (BNC, ±4 V) was connected to a 24-bit external sound card and recorded at a sampling rate of 48 kHz using Cool Edit Pro 2.1 (Syntrillium Software, USA) in uncompressed WAV format. Measurements were conducted at a fixed distance of 1.5 m from unauthorized off-road trails. For each vehicle transit, a 30-second recording was captured, including pre- and post-event background periods.

Spectral analysis was performed using the built-in “Spectral Frequency Display” function in Cool Edit Pro. Since absolute calibration under field conditions is not feasible due to variable surface reflectivity and lack of a reference vibration source, we adopted a comparative approach: for each event, we quantified the relative increase in spectral power (in dBFS, decibels relative to full scale) during vehicle passage compared to the background baseline. This method allowed us to reliably identify and characterize anthropogenic vibrational signals, which is appropriate given our hypothesis focuses on the presence/absence of a detectable vibrational disturbance rather than dose-response relationships.

Statistical analysis

To assess the effect of off-road vehicle activity on fungal fruiting body abundance, we fitted zero-inflated negative binomial generalized linear mixed models (ZINB-GLMM) using the glmmTMB package (v. 1.1.7) in R 4.5.2. The response variable was the daily count of fruiting bodies for each species. Fixed effects included habitat (undisturbed vs. disturbed), mean July air temperature, and relative humidity. Year was included as a random intercept to account for interannual variability. The zero-inflation component was modelled as a function of habitat, given the excess of zero counts in the disturbed transect.

Model diagnostics were performed using the DHARMa package; post-fitting dispersion tests confirmed no residual overdispersion ($p > 0.05$). Incidence Rate Ratios (IRR) with 95% confidence intervals were derived from the conditional (count) part of the model. Statistical significance was set at $p < 0.05$. Sampling effort was identical across transects and years (one 1-km route walked once per day during June-July by a single observer in ~40 minutes); therefore, an offset term was not included.

Results

Seasonality of Fruiting

Analysis of multi-year field data revealed distinct, synchronized fruiting waves for both Boletus edulis and Suillus luteus. Although isolated fruiting bodies were occasionally observed outside these periods, the majority of reproductive output was concentrated in two annual pulses. Mass fruiting, defined as ≥10 fruiting bodies per km of transect per day, occurred predictably during:) late June to late July (summer wave), and late September to mid/late October (autumn wave) (Table 1). The 2024 season was atypical: the autumn fruiting wave was entirely absent, likely due to the anomalous July heat (mean daytime temperature: 26 °C.

Table 1: Dates of mass fruiting periods for Boletus edulis and Suillus luteus (2020-2023)

Year	Dates of the first wave of fruiting	Dates of the second wave of fruiting
2020	17 .06-21.07	14.09-23.10
2021	14.06-17.07	19.09 -11.10
2022	14.06-14.07	14.09-10-11.10
2023	20.06-19.07	17.09-20.10
2024	12.06-14.07	No

Visual observations initiated in 2019 indicated a marked decline in fruiting body abundance of *Boletus edulis* and *Suillus luteus* in areas adjacent to newly established off-road vehicle trails, despite the absence of visible soil disturbance. This reduction was evident even during periods of active regional fruiting and under uniform abiotic conditions (air temperature, humidity, and precipitation) across the shared biotope. Notably, no quantitative census was carried out in 2019; however, substrate vibrations generated by motorcycle traffic were successfully recorded. Examples of vibration signals associated with vehicle movement, including instances of wheel slip, are presented in Figures 2 and 3.

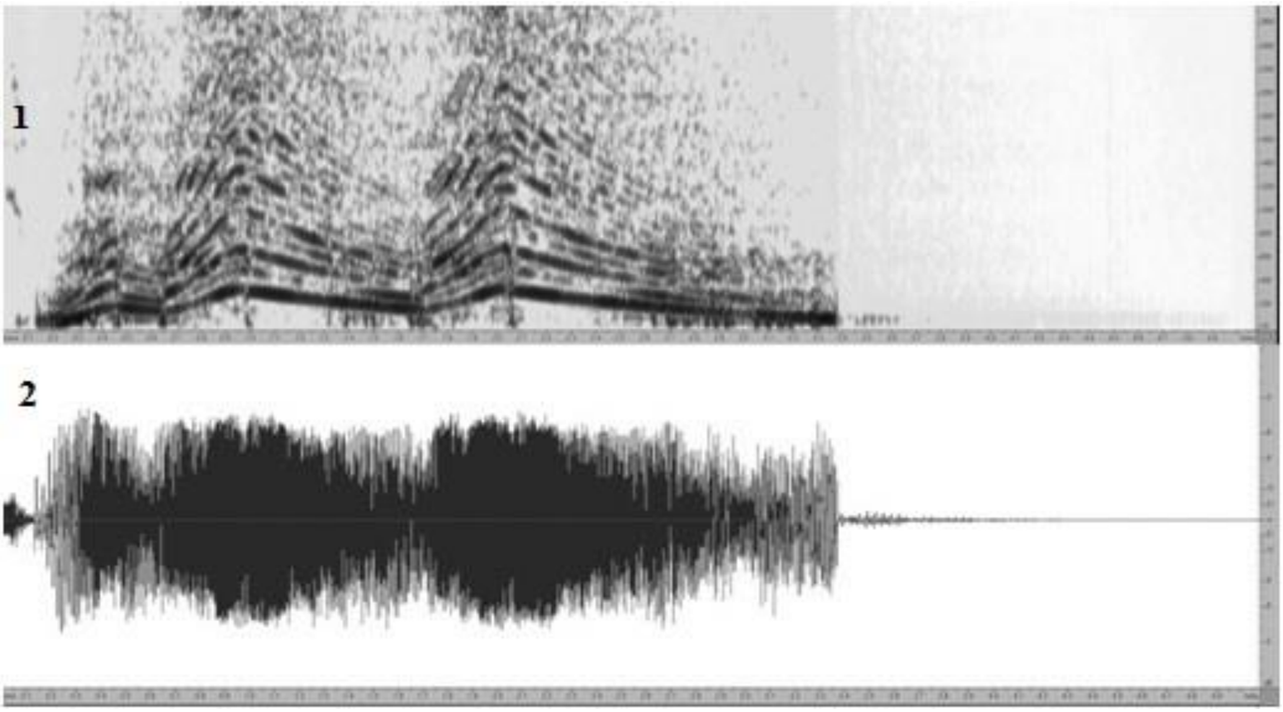

Fig. 2: Substrate-borne vibrations induced by off-road motorcycle transit, recorded 1.5 m from the vehicle trajectory. (1) Sonogram (spectrogram) showing the frequency content and temporal dynamics of the vibrational signal. (2) Oscillogram (time-domain waveform) depicting the amplitude of substrate vibrations over time. The signal clearly shows intense oscillations during vehicle passage, followed by a return to baseline ambient (background) noise after the motorcycle recedes

In 2020, the expansion of off-road motorcycle and ATV trails into previously undisturbed parts of the forest prompted the initiation of a systematic quantitative survey of fungal fruiting bodies in two historically productive zones. Initial observations revealed a marked reduction in mushroom abundance near active vehicle routes, despite the absence of visible soil disturbance (Figures 4-5).

Between 2020 and 2024, the disturbed transect exhibited a consistent and statistically significant decline in *Suillus luteus* fruiting body abundance. While no significant difference was detected in 2020 (mean ± SD: 66 ± 8 vs. 70 ± 10 in control), abundance in the disturbed biotope dropped to 78% of the control value in 2021 (45 ± 10 vs. 58 ± 4), 38% in 2022 (25 ± 5 vs. 65 ± 7), 36% in 2023 (25 ± 5 vs. 70 ± 20), and only 22% in 2024 (14 ± 5 vs. 65 ± 19). Over the same period, abundance in the undisturbed transect remained relatively stable (mean = 65.6, interannual CV < 7.8%). These trends are visually summarized in Figure 4.

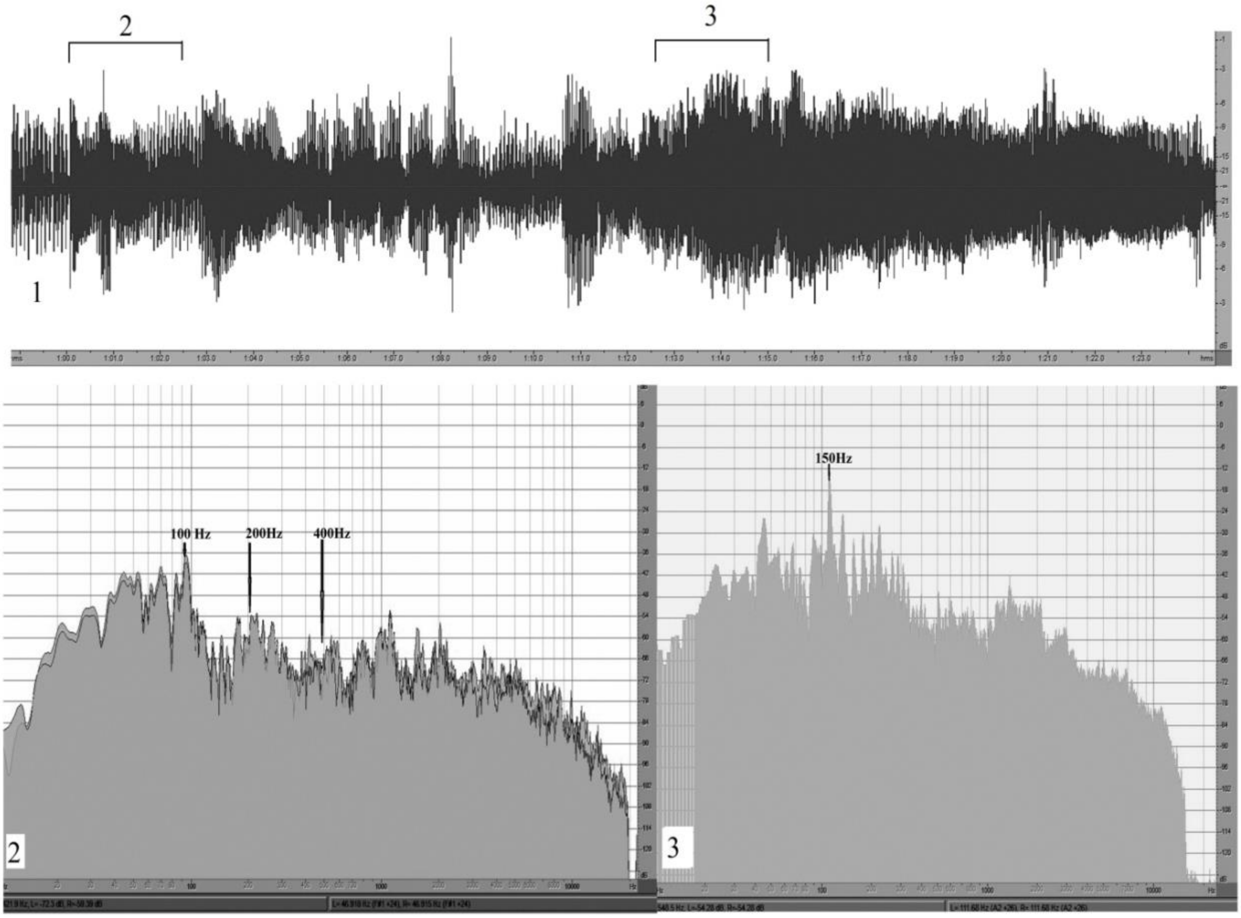

Fig. 3: Substrate-borne vibrations induced by off-road motorcycle transit, recorded 1.5 m from the vehicle trajectory. (1) Oscillogram showing the time-domain amplitude of the vibrational signal. (2, 3) Spectrograms revealing dominant frequency peaks at approximately 100, 150, 200, and 400 Hz

A similar, though more extreme, pattern was observed for *Boletus edulis*. Although both transects showed declining fruiting, the reduction was dramatically more severe in the disturbed zone. By 2024, the disturbed transect recorded near-zero output (0 ± 0), representing functional extirpation, compared to a 77% decline in the control (7 ± 1 vs. 25 ± 3 in 2020). This corresponds to a final abundance of only ~15% of the control value in 2023 and 0% in 2024.

These patterns were formally evaluated using zero-inflated negative binomial generalized linear mixed models (ZINB-GLMM) with year as a random effect. The model confirmed a highly significant negative effect of anthropogenic disturbance on fruiting body counts for both species (*S. luteus*: IRR = 0.59, 95% CI: 0.52-0.66, $p < 0.001$; *B. edulis*: IRR = 0.49, 95% CI: 0.42-0.57, $p < 0.001$). Meteorological variables (July temperature and humidity) were not significant predictors (*p* > 0.05). Full model outputs and confidence intervals are presented in Table 2 and Figures 4-5.

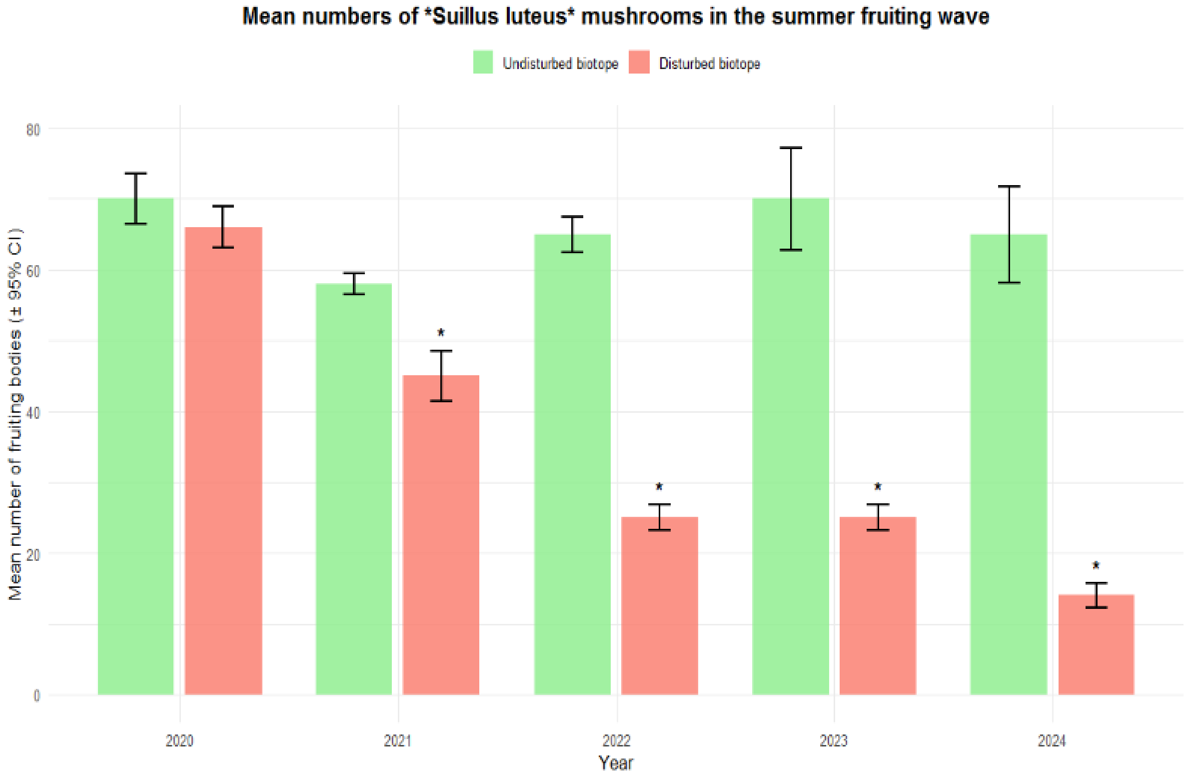

Fig. 4: Mean summer abundance of *Suillus luteus* fruiting bodies (±95% CI) in undisturbed (green) and disturbed (red) transects from 2020 to 2024. Values are based on daily counts (n ≈ 30-37 survey days per year). The consistent reduction in the disturbed transect from 2021 onward reflects the significant negative effect of anthropogenic disturbance identified by the zero-inflated negative binomial GLMM (IRR = 0.59, 95% CI: 0.52-0.66, p < 0.001).

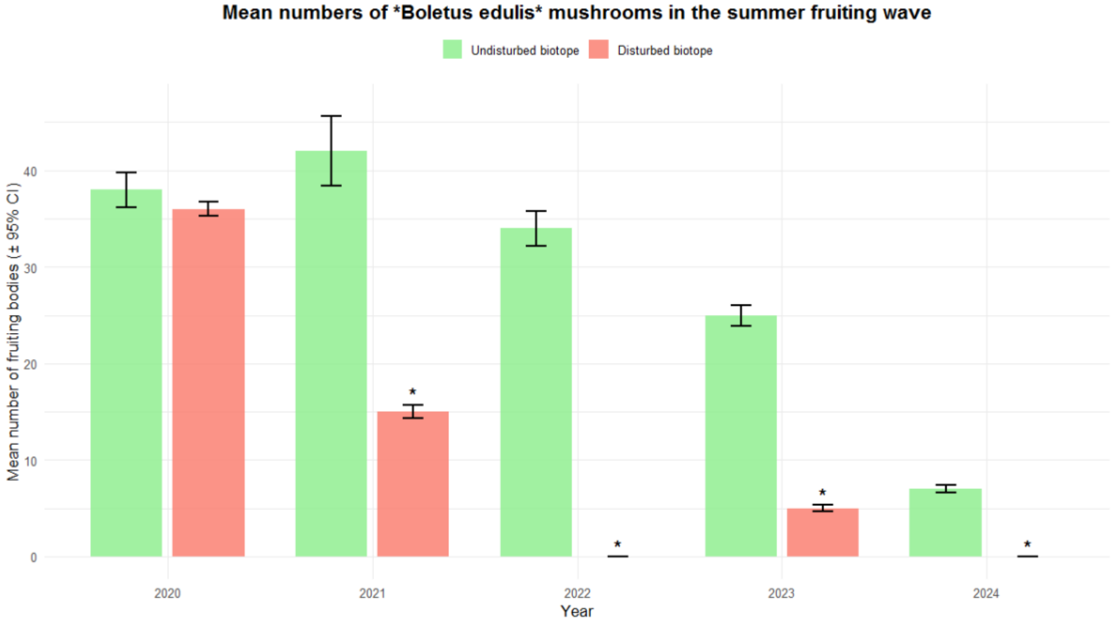

Fig. 5: Mean summer abundance of *Boletus edulis* fruiting bodies (±95% CI) in undisturbed (green) and disturbed (red) transects from 2020 to 2024. The near-complete absence of fruiting in the disturbed transect from 2022 to 2024 underlies the strong negative effect of anthropogenic disturbance identified by the zero-inflated negative binomial GLMM (IRR = 0.49, 95% CI: 0.42-0.57, p < 0.001)

Environmental Factors

To disentangle the effects of anthropogenic disturbance from interannual climatic variability, we fitted zero-inflated negative binomial generalized linear mixed models (ZINB-GLMM) for each species, with year included as a random effect. Fixed predictors were: habitat type (undisturbed vs. disturbed), mean July daytime temperature, and mean July relative humidity. The model confirmed a highly significant negative effect of disturbance on fruiting body abundance for both species: *Boletus edulis*: IRR = 0.49 (95% CI: 0.42-0.57, $p < 0.001$), *Suillus luteus*: IRR = 0.59 (95% CI: 0.52-0.66, $p < 0.001$).

In contrast, meteorological variables showed no statistically significant association with abundance ($p > 0.05$ for both temperature and humidity in both species). Consequently, seasonal temperature and humidity fluctuations (Figure 6) did not correlate with observed changes in fruiting body abundance. Despite noticeable drops in relative humidity (e.g., April 2019, August 2022), no significant decrease in mushroom abundance was observed in control plots. The influence of microclimatic factors was likely negligible, as the sampling sites were in immediate proximity and exhibited no detectable differences in local environmental conditions.

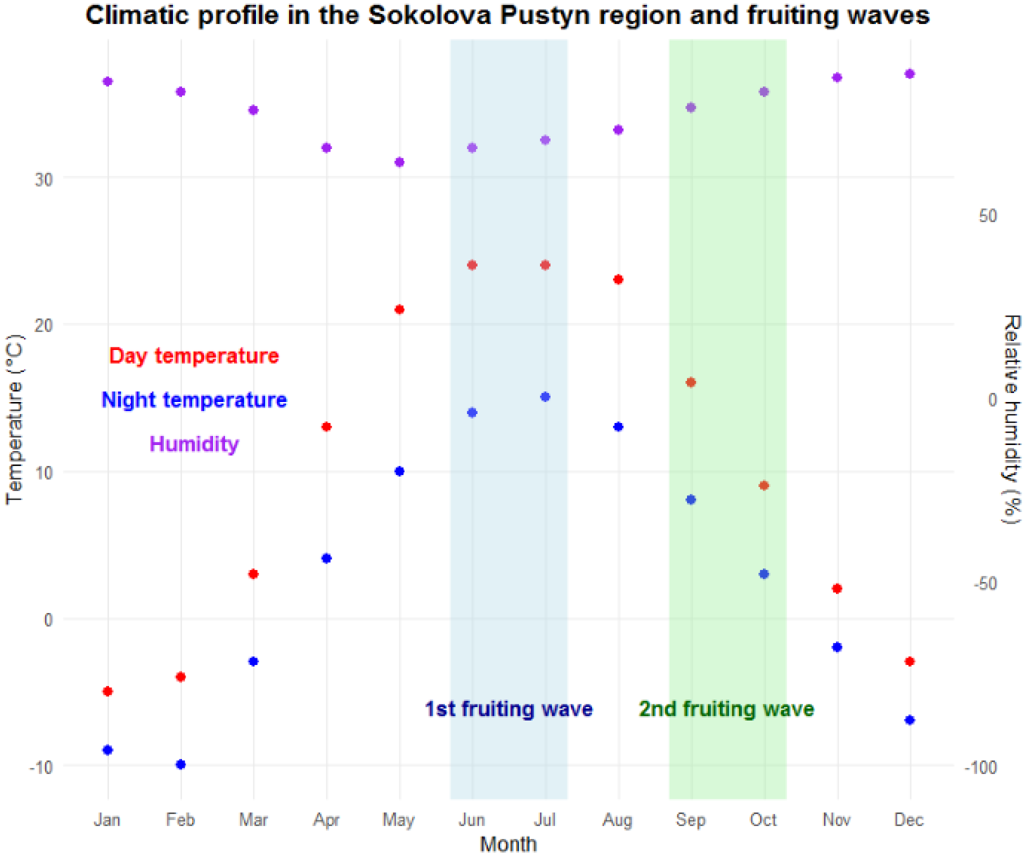

Fig. 6: Climatic profile in the Sokolova Pustyn region (Central Russia), showing monthly mean daytime temperature (red), nighttime temperature (blue), and relative humidity (purple, right axis). Shaded areas indicate periods of peak fruiting activity: light blue for the first wave (June-July) and light green for the second wave (September-October). Data represent long-term averages for the region

For *B. edulis*, the year effect was also significant ($\beta = -0.24$, $p < 0.001$), reflecting a gradual decline across the entire study site over time. Nevertheless, the magnitude of reduction in the disturbed transect far exceeded that in the control, with counts in 2024 approaching zero (mean = 0 ± 0) compared to 7 ± 1 in the undisturbed plot.

No significant difference between habitats was detected in 2020. However, from 2021 onward, abundance in the disturbed transect declined consistently and markedly relative to the control (Figures 4-5, 7), while the undisturbed transect maintained stable fruiting levels (interannual coefficient of variation < 8% for *S. luteus*). These results confirm that off-road vehicle activity, not climate, was the primary driver of reduced fungal productivity.

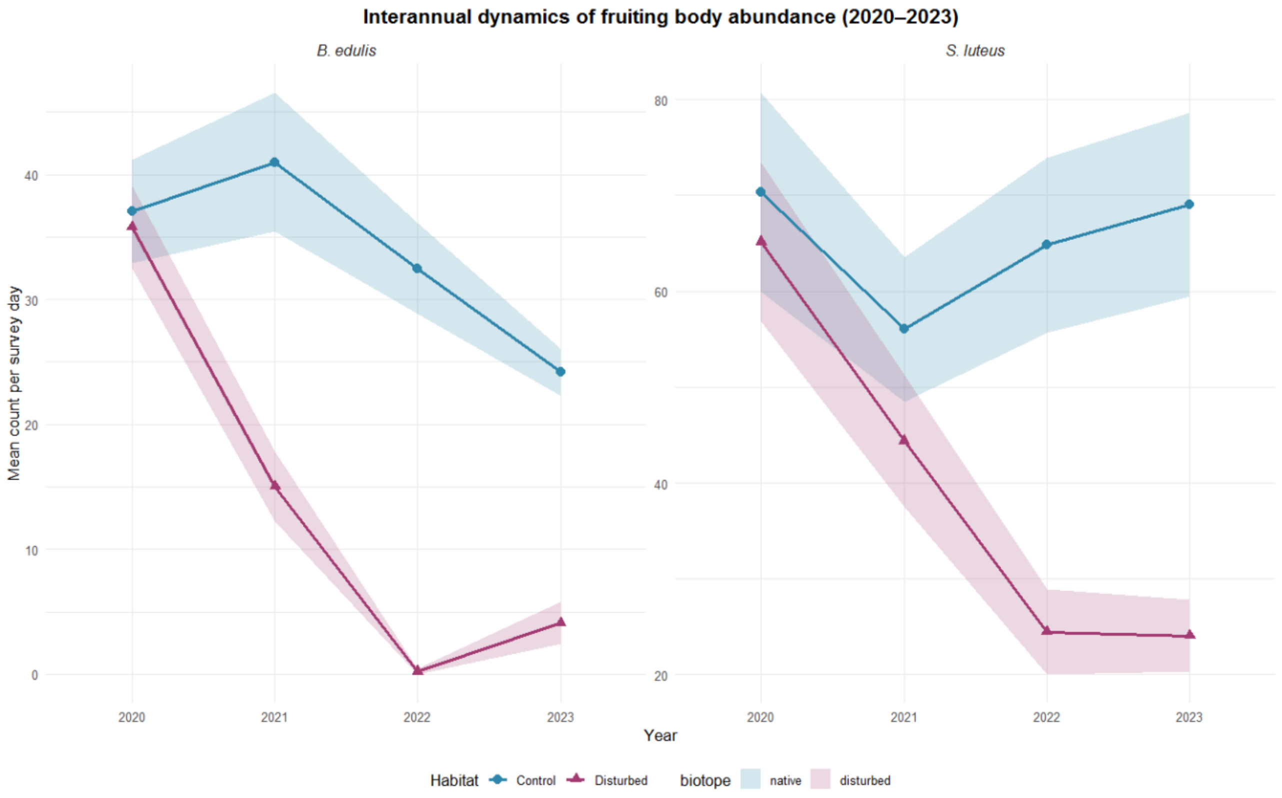

Fig.7: Interannual dynamics of fruiting body abundance (2020-2023) for *Boletus edulis* (left) and *Suillus luteus* (right). Data represent mean counts per survey day in undisturbed (native, light blue) and disturbed (light pink) transects. Solid lines indicate observed means; shaded areas represent 95% confidence intervals

Discussion

Our results demonstrate a consistent and statistically significant decline in the abundance of fruiting bodies of B. edulis and S. luteus in areas adjacent to off-road vehicle trails, with reductions exceeding 50% by 2024. Although mechanical soil disturbance is a well-documented driver of fungal decline [2, 3], no visible trampling, compaction, or erosion was observed within our survey transects. Signs of physical damage were present only near, but not on, one of the transects (see photographs in Supplementary Materials). This indicates that the observed pattern cannot be explained by direct physical disturbance alone.

We hypothesize that substrate-borne vibrations, propagating tens of meters from the trail without leaving surface traces, may act as a cryptic stressor on mycorrhizal networks. This is plausible given the ectomycorrhizal nature of both species and emerging evidence that fungi can perceive mechanical oscillations [15]. Kobayashi et al. [15] proposed that fungi may use substrate vibrations as environmental cues, for instance, to detect treefall events and initiate colonization. However, it should be noted that these findings were obtained on saprotrophic shiitake mushrooms (*Lentinula edodes*), not ectomycorrhizal species.

Anthropogenic vibrations from vehicles are likely to act as noise that masks or disrupts such natural signals, potentially triggering maladaptive responses. Moreover, fungal hyphae are physically integrated with plant root systems and may, in theory, perceive not only mechanical stimuli but also biochemical, electrical, and hydraulic signals transmitted through the mycorrhizal network. It is therefore conceivable that vibrational disturbances interfere with this multimodal communication system, indirectly altering fungal physiology and suppressing fruiting body formation, even in the complete absence of direct physical damage.

Importantly, our statistical analysis confirmed that the observed decline is driven by anthropogenic disturbance rather than climatic variability. Further supporting the potential negative role of vibrations, Tao et al. [16] demonstrated that simulated transport vibrations deteriorate the quality of shiitake mushrooms, indicating that mechanical oscillations can indeed exert adverse effects on fungal biology.

Conclusion

This study provides evidence that off-road recreational vehicle use is associated with a marked decline in the fruiting of ecologically and economically important wild mushrooms, even in the absence of visible soil disturbance. While the exact mechanisms remain to be elucidated, our findings suggest that indirect anthropogenic factors, such as substrate-borne vibrations, may potentially contribute, alongside other unmeasured stressors, to the observed reduction in fungal productivity.

Given the cultural and subsistence value of wild mushroom harvesting across many regions, these results underscore the need for more comprehensive environmental assessments that consider not only physical habitat damage but also less obvious forms of disturbance. We recommend restricting unauthorized off-road access in mycologically sensitive forest areas as a precautionary measure.

Future research will involve controlled laboratory experiments using cultivable fungal species to test the vibrational hypothesis under reproducible conditions. Understanding how substrate vibrations affect fungal development could open new pathways for assessing and mitigating human impacts on forest ecosystems.

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