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Recovery Processes and Delayed Density-Dependent Regulation Reduce Long-Term Insect Damage in Alder Stands

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Abstract

Long-term monitoring data provide an opportunity to distinguish between the prevalence of herbivorous insects and the ecological consequences of their activity. Using observations collected in alder stands within the Polish ICP Forests network during 2013–2025, we investigated temporal patterns of insect-related damage, recovery dynamics, and evidence for delayed density-dependent regulation. Damage severity exhibited strong interannual persistence, although transitions toward lower damage classes occurred more frequently than shifts toward higher classes. Ordinal regression analyses identified contrasting effects of infestation prevalence, with positive contemporaneous effects and negative lagged effects on subsequent damage severity. Plot-level analyses revealed negative feedback and convergence towards an equilibrium damage level, supporting the presence of delayed regulatory processes. Infestation prevalence and damage severity remained strongly associated through time, yet damage declined more rapidly following peak infestation, indicating stronger recovery of ecological impact than of occurrence itself. Spatial analyses revealed persistent clustering of damage levels but comparatively weak spatial structure in annual damage change. Overall, the results demonstrate that persistence, recovery, and delayed feedback jointly shape long-term herbivore impacts in alder ecosystems and highlight the value of assessing both infestation prevalence and damage severity in forest monitoring programmes.

Keywords: forest health; long-term monitoring; insect occurrence; damage severity; density dependence; spatial autocorrelation; damage recovery; alder stands

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1. Introduction

Insect herbivores are among the most important biotic agents affecting the condition and functioning of forest ecosystems. By consuming foliage, they influence primary productivity, nutrient cycling, carbon allocation, and tree growth, thereby affecting ecological processes across multiple spatial and temporal scales [1,2]. Although severe outbreaks can cause substantial defoliation and growth reduction, the ecological consequences of herbivory depend not only on insect occurrence but also on the intensity of damage inflicted on host plants.

Alder-dominated forests constitute a characteristic component of riparian and wetland ecosystems throughout Europe. Black alder (*Alnus glutinosa*) and grey alder (*Alnus incana*)

play important ecological roles through bank stabilization, regulation of hydrological processes, and nitrogen enrichment of nutrient-poor soils through symbiosis with *Frankia* spp. [3]. The health and persistence of alder ecosystems have attracted increasing attention because these forests are exposed to multiple interacting stressors, including pathogens, hydrological alteration, climatic extremes, and herbivorous insects [4,5].

Among the insect herbivores associated with alder, leaf beetles such as *Agelastica alni* and *Plagiosterna aenea* are among the most widespread and ecologically significant species [6]. These insects complete one generation per year, feed predominantly on alder foliage, and may locally reach high population densities. Their feeding activity produces characteristic foliar damage that can be readily assessed during forest health monitoring and is therefore commonly used as an indicator of herbivore pressure.

Long-term forest monitoring commonly records both insect presence and visible damage symptoms, although these variables do not necessarily describe the same ecological processes. While occurrence reflects the spatial distribution of herbivore populations, damage severity represents the realized impact of feeding activity on host trees. Consequently, variation in these indicators may reveal different mechanisms governing forest health and ecosystem responses to herbivory. However, persistent occurrence does not necessarily translate into persistent ecological impact. Growing evidence indicates that occurrence and damage may follow different temporal trajectories [7,8]. Similar herbivore densities can generate contrasting levels of injury depending on host resistance, compensatory responses, natural-enemy activity, and environmental conditions [2,9,10]. Consequently, occurrence alone may not provide a complete description of herbivore impacts on forest ecosystems [11].

A range of ecological processes may weaken the relationship between herbivore occurrence and observed damage levels. Host trees may increase resistance following repeated attack [2,12], natural enemies can suppress herbivore populations in a density-dependent manner [9,13], and compensatory growth may reduce the visible consequences of defoliation despite continued feeding pressure [14,15]. As a result, the presence of herbivores does not always translate directly into severe foliage damage.

Understanding the relationship between insect occurrence and damage severity is particularly important in the context of forest monitoring and forest health assessment. Different indicators may capture different ecological processes and may therefore provide contrasting assessments of ecosystem condition [16]. Whereas occurrence primarily reflects the distribution and persistence of herbivore populations, damage severity describes the extent of observed foliar damage associated with herbivore activity. Distinguishing between these dimensions is necessary for interpreting long-term monitoring data and for evaluating whether persistent insect occurrence is accompanied by sustained damage levels. Management decisions and risk assessments are often based on indicators of pest presence, yet persistent occurrence does not necessarily imply persistent damage. Quantifying the relationship between occurrence and damage may therefore improve interpretation of monitoring data and contribute to more robust assessments of forest condition.

Spatial patterns may provide an additional perspective on the relationship between insect occurrence and damage severity. Herbivore occurrence is primarily determined by processes influencing population distribution and dispersal, whereas damage severity may additionally depend on local environmental conditions, host quality, stand structure, and plant responses to herbivory. Consequently, two areas with similar levels of insect occurrence may exhibit different levels of observed damage. If such local factors remain relatively stable through time, damage severity may display spatial structures that differ from those observed for occurrence. Examining spatial patterns therefore provides an

opportunity to assess whether the distribution of herbivores and the distribution of their associated damage are governed by similar or distinct ecological processes.

Long-term datasets are especially valuable for investigating such relationships because short-term studies may fail to separate transient fluctuations from sustained ecological trends. The International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests) provides one of the largest standardized forest monitoring datasets in Europe, enabling analyses of herbivore occurrence and tree condition over extended periods and broad geographic scales [17,18].

The primary objective of the study was to identify large-scale temporal and spatial patterns in damage dynamics across the monitoring network rather than to estimate tree-level random effects. Consequently, analyses were based on population-averaged relationships using lagged predictors and plot-level summaries where appropriate.

Using a 13-year dataset from the Polish ICP Forests network, we examined long-term dynamics of insect-induced damage in alder stands and evaluated its relationship with insect occurrence. Specifically, we tested the following hypotheses: (H1) damage severity exhibits temporal persistence, but weaker than the persistence previously observed for insect occurrence; (H2) damage dynamics are regulated by delayed density-dependent feedback associated with local infestation intensity; (H3) damage severity and insect occurrence exhibit similar long-term trajectories but differ in their short-term regulatory dynamics; and (H4) spatial patterns of damage differ from those observed for occurrence, reflecting distinct ecological processes governing distribution and impact.

2. Materials and Methods

2.1. Data Collected from the ICP Forests Monitoring

The analyses were performed using observations obtained from the European ICP Forests network, a coordinated monitoring system designed to provide long-term information on forest condition across a broad geographic range. The network applies harmonized field procedures and quality-control standards, allowing consistent evaluation of ecological patterns among regions and years [17,18]. The monitoring framework integrates repeated assessments of tree vitality, crown condition, biotic damage, and other indicators describing forest responses to environmental pressures. Because the same methodological principles are applied throughout the network, the resulting datasets are well suited for investigating large-scale temporal and spatial variation in forest health [18].

In Poland, annual forest condition assessments are performed on a network of permanent observation plots distributed throughout the country [19]. Assessments were conducted once per year during the growing season following the standardized ICP Forests protocol. Each plot contains a fixed set of monitored trees that are evaluated repeatedly using harmonized field procedures. Recorded variables include crown condition, defoliation, discoloration, biotic and abiotic damage, and a range of indicators describing tree vitality and ecosystem health.

The present study focused on alder-dominated stands monitored within the Polish ICP Forests network between 2013 and 2025. The dataset comprised 176 monitoring locations, although not all plots were surveyed throughout the entire study period because some locations entered or left the monitoring network over time. A subset of 105 locations contained complete observations across all years and was used to verify the robustness of the analyses. Results obtained for the complete and reduced datasets were highly consistent; therefore, all analyses presented in this study are based on the full dataset.

In Poland, three native alder species occur: black alder (*Alnus glutinosa*), grey alder (*Alnus incana*), and green alder (*Alnus viridis*). The monitored stands were overwhelmingly dominated by black alder (*A. glutinosa*; 94.7% of observations), whereas grey alder

(*A. incana*) accounted for 5.3% of observations. Green alder (*A. viridis*) was not represented in the ICP Forests plots included in this study. According to ICP Forests protocols, assessments are conducted on dominant trees aged at least 21 years; therefore, the analyses primarily characterize mature alder stands rather than young regeneration stages.

The ICP Forests monitoring network includes permanent plots distributed across a broad range of environmental conditions representative of Polish forests. Protection status and management category were not used as selection criteria in the present study, and the analyses were therefore intended to characterize large-scale patterns across the monitoring network as a whole.

Annual surveys recorded visible symptoms of insect feeding on alder foliage. Damage observations were collected using the standard ICP Forests classification system, in which increasing classes correspond to progressively larger proportions of affected leaf area. Within the present study, these observations were interpreted as indicators of the ecological consequences of herbivore activity rather than direct measures of insect abundance. The original assessment scale comprised eight ordered classes representing different levels of foliage injury. To improve interpretability and ensure adequate sample sizes within categories, the original classes were merged into four broader levels describing absent, low, moderate, and high damage. Plot-level impact was subsequently characterized using the average damage category calculated from all assessed trees within a given location and survey year. To describe the extent of infestation, an additional variable was calculated as the proportion of assessed trees exhibiting detectable insect damage within each plot. This measure was used to characterize infestation prevalence across the monitoring network. Consequently, the analyses considered two complementary descriptors of herbivore pressure: one reflecting how widespread damage symptoms were among trees and another representing the intensity of their ecological effects. Although both variables originated from the same field observations, they summarize different attributes of the herbivory process. Infestation prevalence describes the frequency of affected trees within a stand, whereas damage severity quantifies the magnitude of injury recorded on individual hosts. The two metrics were therefore analysed jointly to distinguish patterns associated with herbivore distribution from those associated with realized ecological impact.

2.2. Analysis of Tree Damage Severity

The primary focus of this study was the dynamics of insect-induced damage severity, which was used as an indicator of the realized ecological impact of herbivory on host trees. Analyses conducted at the level of individual trees allowed assessment of damage persistence, recovery processes, and relationships between local infestation intensity and subsequent damage severity.

The recoded damage categories described in Table 1 were used in all subsequent tree-level analyses.

Table 1. Distribution of damage severity categories after recoding. Values represent percentages of all observations.

Damage Category	Damage Range [%]	Observations [%]
No damage	0%	22.9
Low	1%–10%	29.8
Moderate	11%–20%	34.1
High	21%–100%	13.2

These recoded categories were subsequently used in transition analyses, ordinal regression models, and all tree-level assessments of damage dynamics.

2.2.1. Damage State Transitions and Year-to-Year Persistence

To investigate the dynamics of damage severity at the level of individual trees, we analyzed year-to-year transitions between damage classes (Table 1). The recoded damage variable (four ordinal categories) was treated as a discrete state, and transitions were examined within a first-order Markov framework.

For each tree, the damage state was compared with its state in the previous year. Transition probabilities were estimated using contingency tables normalized by the previous state, yielding empirical estimates of conditional probabilities:

$$p_{ij} = P(Y_t = j \mid Y_{t-1} = i) = \frac{n_{ij}}{\sum_k n_{ik}}, \quad (1)$$

where p_{ij} is the probability of transition from damage state i to damage state j between consecutive years.

To further assess the role of year-to-year persistence and long-term trends, we fitted an ordinal logistic regression model in which the damage class was modeled as a function of both the damage state in the previous year and time (year):

$$\text{logit}\big(P(Y_t \leq k)\big) = \theta_k - (\beta_1 \cdot Y_{t-1} + \beta_2 \cdot \text{year}), \quad (2)$$

where Y_t is the damage class at time t, Y_{t-1} is the lagged damage class, and θ_k are threshold parameters separating ordinal categories.

2.2.2. Effects of Local Infestation Intensity on Damage Severity

To evaluate whether damage severity depends on local herbivore pressure, we incorporated a measure of infestation intensity into the modelling framework. For each monitoring location and year, infestation intensity was quantified as plot-level occupancy, calculated as the proportion of monitored trees exhibiting insect occurrence within a given plot and year (O_t).

A lagged occupancy variable (O_{t-1}) was calculated to represent herbivore pressure experienced during the previous year. Both occupancy measures were assigned to individual-tree observations according to their location and year.

As in previous analyses, a lagged damage variable (Y_{t-1}) was included to account for persistence of damage severity at the level of individual trees.

Damage severity was analysed using ordinal logistic regression:

$$\text{logit}\big(P(Y_t \leq k)\big) = \theta_k - (\beta_1 \cdot Y_{t-1} + \beta_2 \cdot O_{t-1} + \beta_3 \cdot O_t), \quad (3)$$

where Y_t denotes the damage class at time t, Y_{t-1} is the previous damage class, O_t and O_{t-1} represent current and lagged plot-level occupancy, and θ_k are threshold parameters separating ordinal categories.

This formulation allows the disentangling of immediate and delayed effects of insect population dynamics on damage progression.

2.2.3. Model Comparison

To assess the relative importance of temporal trends, year-to-year persistence, and local infestation intensity in explaining damage severity, a set of ordinal regression models of increasing complexity was compared, including models with time only, lagged damage with time, and a full model incorporating lagged damage and density terms.

Model performance was evaluated using the Akaike Information Criterion (AIC) and McFadden's pseudo-R^2, allowing comparison of model fit and explanatory power.

Odds ratios (OR) derived from model coefficients were used to facilitate interpretation of effect sizes.

Because monitoring plots were surveyed repeatedly through time, temporal dependence was addressed explicitly through lagged predictors representing previous damage severity (Y_{t-1}) and previous-year occupancy (O_{t-1}). These variables were incorporated directly into the regression models to account for year-to-year persistence in damage dynamics.

Potential spatial dependence was evaluated separately using Moran's I analyses (see Section 3.6) This approach allowed the assessment of large-scale spatial structure while focusing the regression analyses on population-averaged relationships.

In addition, model performance was evaluated in terms of the ability to reproduce the observed distribution of damage severity classes by comparing predicted and observed class frequencies.

2.2.4. Relationship Between Occurrence and Damage

To assess the degree of coupling between herbivore occurrence and ecological impact, temporal trajectories of occupancy and damage severity were compared at the annual scale.

Annual mean occupancy and annual mean damage severity were calculated for each year and compared using annual trajectories and Pearson correlation analysis. Differences between temporal trajectories were used as an indicator of potential decoupling between herbivore occurrence and ecological impact. Differences between standardized trajectories were evaluated descriptively and used to identify long-term divergence between infestation and ecological impact.

In addition, a logistic regression model was fitted in which current insect occurrence ($Y_t = 1$) was modeled as a function of both lagged occurrence (Y_{t-1}) and lagged damage severity (D_{t-1}):

$$\text{logit}(P(Y_t = 1)) = \beta_0 + \beta_1 Y_{t-1} + \beta_2 D_{t-1}. \quad (4)$$

This analysis was used to determine whether damage severity provides information about future occurrence beyond the persistence of occurrence itself.

2.3. Damage Dynamics and Delayed Density Dependence

To investigate the processes governing temporal changes in ecological impact, damage dynamics were analyzed at the plot level. For each monitoring location and year, mean damage severity (D_t) was calculated as the average damage class across all assessed trees.

Year-to-year changes in damage severity were quantified as:

$$\Delta D = D_t - D_{t-1}, \quad (5)$$

where D_t denotes mean damage severity in year t and D_{t-1} represents the corresponding value in the preceding year.

This formulation allows evaluation of both the direction and magnitude of temporal changes in damage. Positive values of ΔD indicate increasing damage severity, whereas negative values correspond to recovery or declining ecological impact.

To assess whether damage dynamics were regulated by density-dependent feedback, relationships between ΔD, previous damage severity (D_{t-1}), and local infestation intensity were examined. Local infestation intensity was represented by plot-level occupancy, calculated as the proportion of trees exhibiting insect occurrence within a given location and year.

Particular attention was given to the effects of lagged occupancy (O_{t-1}), which represents herbivore pressure experienced during the previous year. A significant negative

relationship between ΔD and lagged occupancy would indicate delayed density-dependent regulation, whereby intense infestation is followed by a subsequent reduction in damage severity.

Linear regression models were fitted to evaluate the effects of previous damage severity (D_{t-1}), lagged occupancy (O_{t-1}), and year on damage dynamics (ΔD). In addition, damage-change distributions were examined across the full range of initial damage levels in order to identify equilibrium conditions and determine whether damage tended to converge toward a stable long-term state.

An equilibrium damage level was defined as the value of D_{t-1} for which the expected year-to-year change in damage severity approached zero:

$$E(\Delta D) = 0. \quad (6)$$

This approach allows distinction between systems characterized by cumulative damage accumulation and those exhibiting compensatory processes that promote recovery following periods of elevated herbivore pressure.

2.4. Spatial Structure of Damage Dynamics

Spatial autocorrelation of damage severity was quantified using Moran's I statistic [20].

For each year, mean damage severity was calculated for every monitoring location and used as the input variable for spatial analyses. Because damage classes are ordinal, plot-level mean damage was used as an approximation of local damage intensity.

Spatial autocorrelation was evaluated both for damage severity itself (D) and for year-to-year changes in damage severity:

$$\Delta D = D_t - D_{t-1}. \quad (7)$$

Spatial weights were constructed using a k-nearest-neighbours framework with $k = 5$. Significance testing was based on permutation-derived null distributions.

Regional variation in damage severity was visualized by generating continuous prediction surfaces using inverse distance weighting (IDW). Because the interpolation was intended only to support graphical interpretation, these surfaces were not used for statistical inference.

2.5. Software and Computational Tools

Data processing, statistical modelling, and spatial analyses were conducted in Python (version 3.12). Data manipulation was performed using `numpy` and `pandas` [21,22]. Ordinal and generalized linear regression models were fitted using `statsmodels` [23], whereas spatial autocorrelation analyses were performed with `libpysal` and `esda` within the PySAL ecosystem [24]. For visualization of spatial patterns, inverse distance weighting (IDW) interpolation was implemented in Python.

3. Results

3.1. Long-Term Trends in Damage Severity

Long-term changes in damage severity were examined to determine whether the ecological impact of herbivorous insects remained stable throughout the monitoring period.

The distribution of damage categories exhibited a clear shift toward lower levels of damage over time (Figure 1). This trend was characterized by a declining proportion of trees classified in the moderate- and high-damage categories and a corresponding increase in the proportion of trees exhibiting low levels of damage.

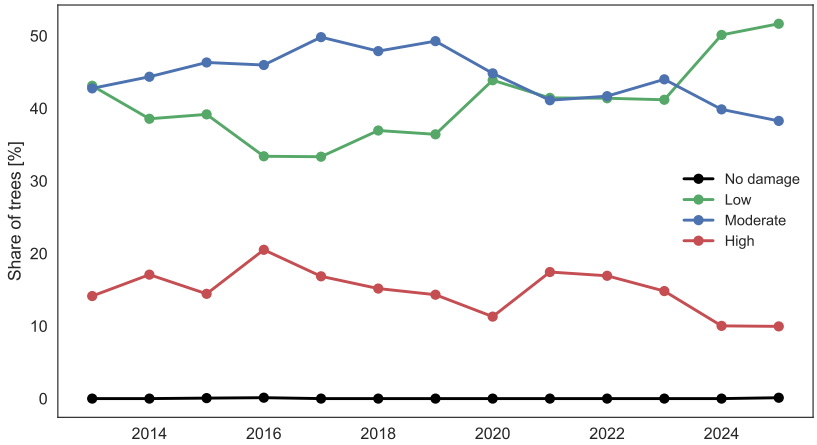


Figure 1. Temporal changes in the proportion of trees assigned to each damage severity category during the study period. Categories represent the recoded ICP Forests damage classes used in the analyses.

The observed pattern was supported by Spearman rank correlation analyses. The proportion of trees in the low-damage category increased significantly through time ($\rho = 0.076$, $p < 0.001$), whereas the proportions of trees with moderate and high damage declined ($\rho \approx -0.044$, $p < 0.001$). No significant temporal trend was detected for the no-damage category.

These results indicate a gradual reduction in the severity of insect-induced damage over the study period. Although damage remained common across the monitoring network, the frequency of more severe damage classes declined steadily, suggesting a long-term decrease in the realized ecological impact of herbivory.

The shift toward lower damage classes was consistent with the negative temporal effect detected in subsequent ordinal regression analyses (see Section 3.2), indicating that the declining trend occurred independently of short-term year-to-year fluctuations. Overall, the results suggest that recovery processes slightly exceeded damage accumulation during the monitoring period, resulting in progressively lower levels of damage severity across alder stands.

3.2. Persistence and Recovery of Damage

To investigate the mechanisms underlying long-term changes in damage severity, year-to-year transitions between damage categories were analyzed at the level of individual trees.

Transitions between consecutive years revealed strong persistence of damage severity (Table 2). Most trees remained in the same damage category from one year to the next, as indicated by the high probabilities along the diagonal of the transition matrix. Depending on the initial damage level, the probability of remaining in the same category ranged from 69% to 77%, demonstrating substantial temporal stability of damage states.

Despite this strong persistence, transitions toward lower damage categories were generally more frequent than transitions toward higher categories. This asymmetry was particularly pronounced among heavily damaged trees. Approximately 31% of trees in the highest damage category shifted to lower damage levels in the following year, whereas transitions from moderate to high damage were relatively rare (6%). Similarly, transitions from low to moderate damage occurred less frequently than retention within the low-damage category. These patterns indicate that transitions toward lower damage categories were more common than transitions toward higher categories.

Table 2. Transition probabilities between damage severity classes (%).

Previous ↓ / Current →	No	Low	Moderate	High
No damage	73.5	11.5	12.1	3.0
Low damage	8.2	76.9	10.4	4.5
Moderate	6.5	12.0	75.4	6.2
High damage	3.9	8.0	19.1	69.0

The ordinal regression analysis confirmed the dominant role of previous damage severity in determining current damage levels. Damage severity in the previous year exerted a strong positive effect on the probability of higher damage in the current year (OR = 10.04, 95% CI: 9.65–10.44, $p < 0.001$), indicating substantial year-to-year persistence at the level of individual trees.

In addition to this persistence effect, a weak but significant negative effect of year was detected (OR = 0.98, 95% CI: 0.97–0.98, $p < 0.001$), demonstrating a gradual decline in damage severity throughout the monitoring period independent of the previous damage state.

Model comparison supported this interpretation (Table 3). The full model, incorporating previous damage severity together with current and lagged occupancy, provided the best fit to the data (AIC = 49 501; pseudo-$R^2 = 0.334$). Models omitting either persistence or occupancy variables exhibited substantially lower explanatory power, indicating that both processes are required to explain observed variation in damage severity.

Table 3. Comparison of ordinal regression models explaining damage severity. Values are presented as odds ratios (OR) with 95% confidence intervals (CI). Pseudo-R^2 values correspond to McFadden's measure.

Predictor	OR	95% CI
Previous damage (Y_{t-1})	10.04	9.65–10.44
Year	0.98	0.97–0.98
Lagged occupancy (O_{t-1})	0.06	0.05–0.07
Current occupancy (O_t)	68.70	59.45–79.44
AIC	49,501	
Pseudo-R^2	0.334	

All effects statistically significant ($p < 0.001$).

Taken together, these results indicate that damage severity is characterized by strong short-term persistence, but also by a consistent tendency toward recovery. Although individual trees often remained within the same damage category between years, transitions toward lower damage levels occurred more frequently than transitions toward higher levels. Consequently, reductions in observed damage severity occurred more frequently than increases in damage severity, contributing to the long-term decline in severe damage observed across the monitoring network.

3.3. Infestation-Dependent Regulation of Damage

To assess the role of herbivore pressure in shaping damage severity, we examined the effects of both current and lagged occupancy on damage dynamics.

The ordinal regression models revealed a strong contrast between immediate and delayed effects of infestation intensity. Current occupancy (O_t) exhibited a very strong positive association with damage severity(OR = 68.70, 95% CI: 59.45–79.44), indicating that trees located in plots with a high proportion of infested trees were substantially more likely to experience severe damage. This result demonstrates that damage responds rapidly to

local infestation intensity and increases as herbivore pressure becomes more widespread within a plot.

Although the estimated odds ratios were large, they reflect the fact that occupancy was expressed as a proportion ranging from 0 to 1, so model coefficients correspond to changes across the full occupancy gradient rather than unit changes in the number of infested trees.

In contrast, lagged occupancy (O_{t-1}) was negatively associated with current damage severity (OR = 0.06, 95% CI: 0.05–0.07). Consequently, plots experiencing high infestation intensity in one year tended to exhibit lower levels of damage in the following year. This pattern is consistent with a delayed density-dependent response, although the underlying mechanisms cannot be identified directly from the available monitoring data.

Previous damage severity remained an important predictor of current damage levels (OR $\approx$ 10.0, $p < 0.001$), confirming the strong persistence of damage at the level of individual trees. However, the opposing effects of current and lagged occupancy indicate that local herbivore pressure influences damage through both immediate and delayed pathways.

Model comparison further supported this interpretation (Table 3). The full model, incorporating previous damage severity together with current and lagged occupancy, provided the best fit to the data (AIC = 49,501; McFadden's pseudo-R^2 = 0.334). Models omitting either persistence or occupancy variables exhibited substantially poorer performance, indicating that both processes contribute to observed variation in damage severity.

Taken together, these results suggest that damage severity is shaped by local persistence and patterns consistent with density-dependent regulation. High occupancy promotes severe damage in the current year, whereas high occupancy in the previous year is associated with reduced damage severity in subsequent years. The coexistence of positive immediate effects and negative delayed effects suggests that ecological impact is regulated by feedback mechanisms operating across multiple years rather than by contemporaneous infestation intensity alone.

3.4. Damage Dynamics and Delayed Density Dependence

To characterize temporal variation in damage severity, annual changes in mean damage (ΔD) were evaluated at the plot level. Plot–year combinations represented by fewer than 10 monitored trees were excluded to minimize the influence of sampling variability.

A clear pattern of negative feedback was observed (Figure 2a). Plots characterized by low damage severity tended to exhibit increases in damage during the following year, whereas plots with high levels of damage more frequently experienced subsequent declines.

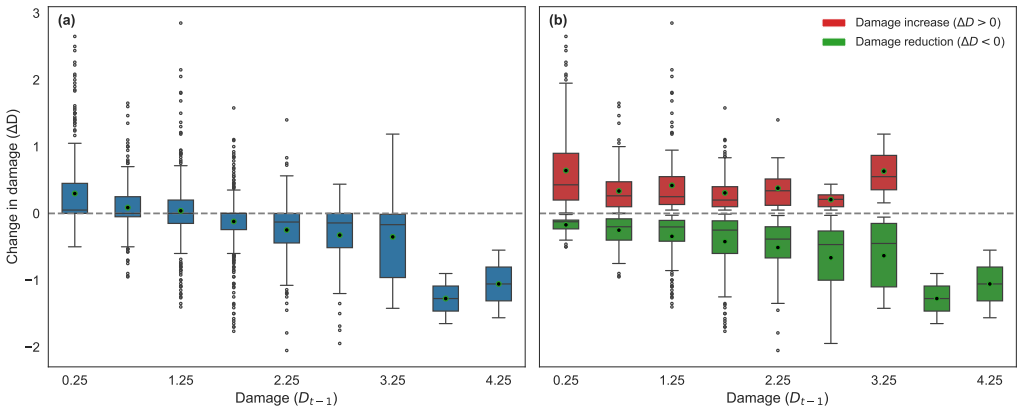


Figure 2. Relationship between annual changes in damage severity (ΔD) and initial damage levels observed in the preceding year (D_{t-1}). Panel (**a**) shows the distribution of year-to-year changes across successive damage classes, whereas panel (**b**) separates positive and negative changes in damage severity. Values along the x-axis correspond to the midpoints of the respective damage intervals.

The strongest changes occurred at the extremes of the damage gradient. Lightly damaged plots generally exhibited positive values of ΔD, whereas heavily damaged plots were characterized by negative values of ΔD. Expected year-to-year change approached zero at an intermediate damage level of approximately $D^* \approx 1.4$.

3.5. Relationship Between Occurrence and Damage

To evaluate the relationship between herbivore occurrence and ecological impact, annual trajectories of occupancy and damage severity were compared (Figure 3).

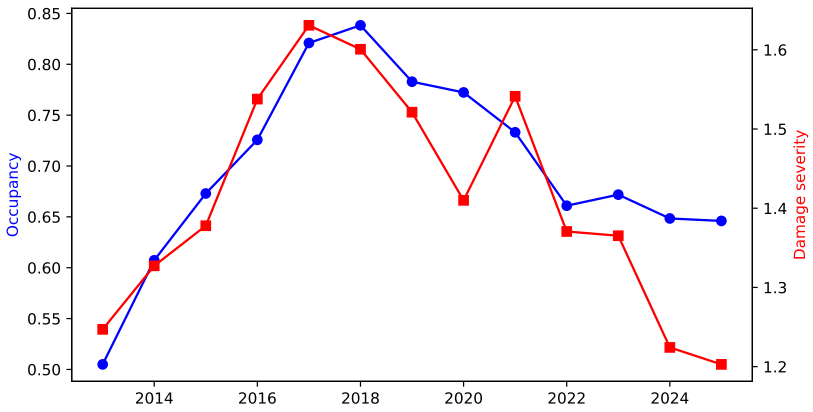


Figure 3. Temporal trajectories of insect occurrence and damage severity across the monitoring period. Occurrence is expressed as the proportion of trees exhibiting insect-induced damage, whereas damage severity corresponds to the annual mean damage level recorded within the monitoring network.

Occupancy and damage severity exhibited strongly correlated long-term trajectories (Pearson's $r = 0.84$, $p < 0.001$). Both indicators increased during the first part of the study period, reached maximum values around 2017–2018, and subsequently declined. This pattern indicates that broad-scale temporal changes in ecological impact closely tracked changes in herbivore occurrence.

Despite this overall correspondence, differences emerged following the population peak. Damage severity began to decline slightly earlier than occupancy and decreased more rapidly during the later years of the study. Consequently, damage severity remained lower than expected from occupancy levels throughout most of the post-peak period. The divergence between occupancy and damage became particularly pronounced during the final years of monitoring, although an isolated increase in damage severity was observed in 2021.

The logistic regression analysis confirmed that previous occurrence was the dominant predictor of current occurrence (OR = 38.74, 95% CI: 35.43–42.37, $p < 0.001$). In contrast, damage severity in the previous year did not significantly affect subsequent occurrence (OR = 1.02, 95% CI: 0.98–1.07, $p = 0.331$).

Taken together, these results indicate that occupancy and damage severity remain closely coupled at broad temporal scales but differ in their post-peak dynamics. While herbivore occurrence and ecological impact generally followed similar long-term trajectories, damage severity exhibited stronger recovery following periods of elevated infestation.

3.6. Spatial Structure of Damage

Damage severity displayed a clear and persistent spatial structure throughout the study period (Figure 4). Moran's I values were consistently positive (mean = 0.31), indicating significant clustering of similar damage levels among neighbouring monitoring plots. Despite interannual variation in autocorrelation strength, regional patterns of damage remained evident across the monitoring network.

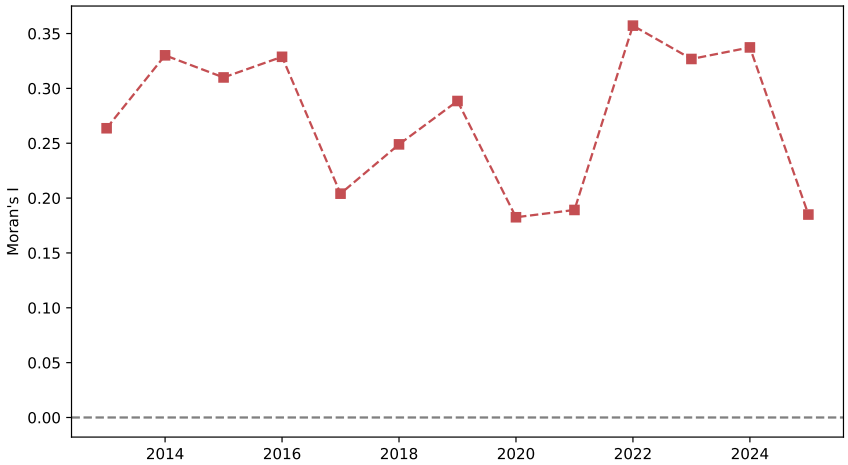


Figure 4. Variation in Moran's I for mean damage severity at the plot level versus year of observation.

The interpolated maps supported these findings by revealing stable geographical variation in damage severity across the monitoring network (Figure 5). Regions characterized by relatively high or low damage tended to remain similar through time.

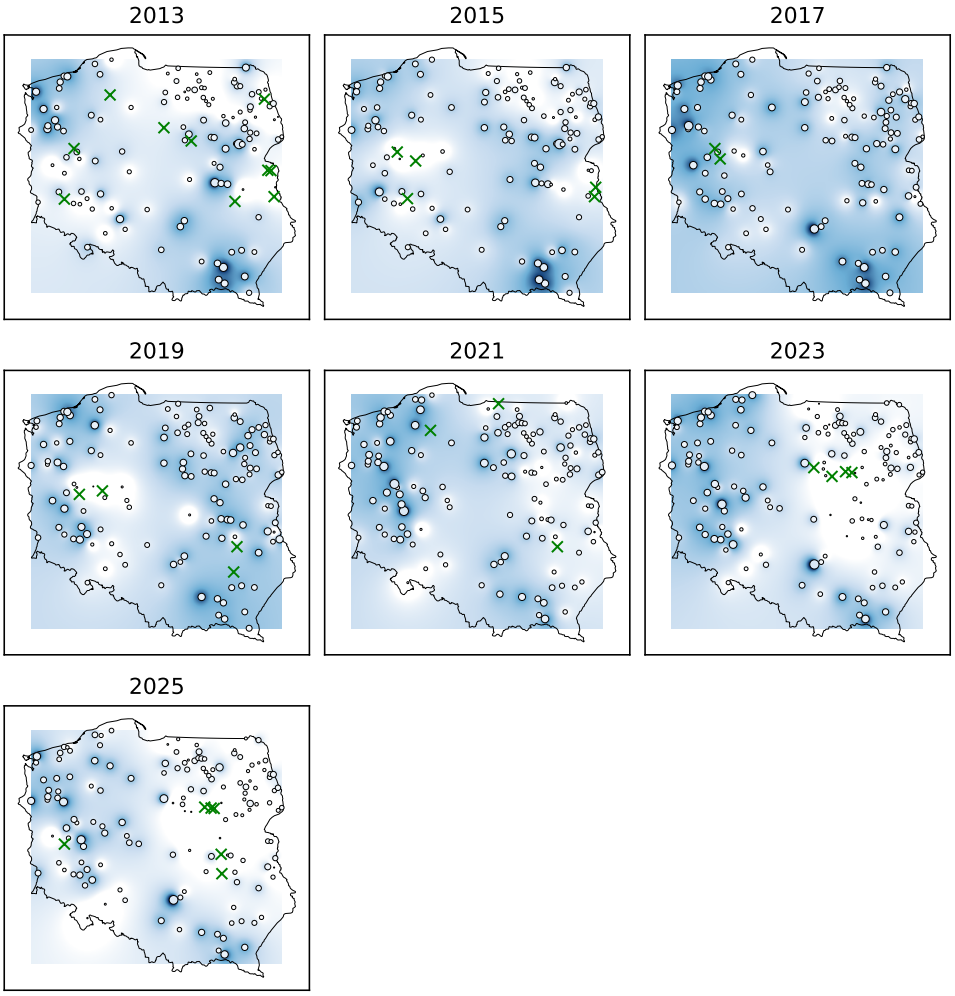


Figure 5. Geographical patterns of mean damage severity recorded in alder stands during selected years of the monitoring period. Continuous surfaces were generated using inverse distance weighting (IDW) interpolation of plot-level observations. Monitoring locations are represented by circles scaled and coloured according to mean damage severity, whereas green crosses indicate plots without recorded insect-induced damage.

Compared with damage severity itself, annual changes in damage (ΔD) exhibited much weaker spatial autocorrelation (Figure 6). Moran's I values for ΔD remained consistently low, suggesting only limited spatial coordination of damage dynamics among neighbouring plots.

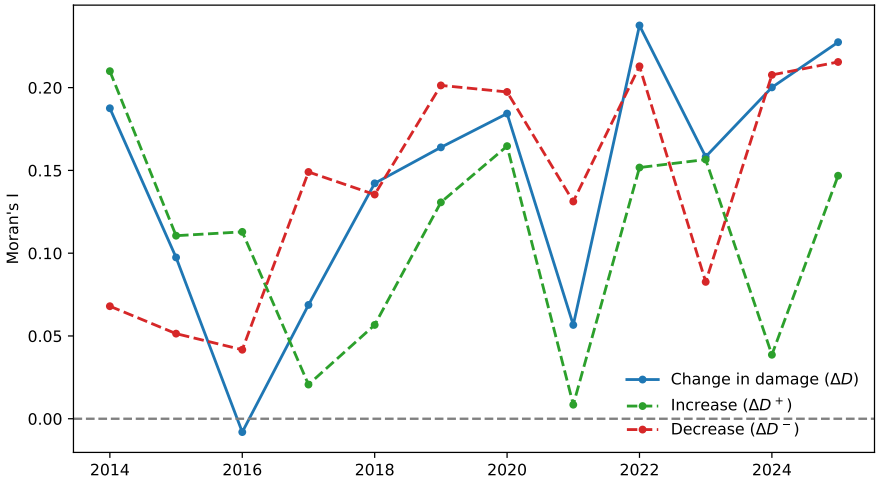


Figure 6. Annual variation in spatial autocorrelation of damage-severity dynamics (ΔD) across the monitoring network. Moran's I values are shown for all year-to-year changes combined, as well as separately for positive and negative changes in damage severity.

This interpretation is consistent with additional analyses of turnover dynamics, which revealed only weak and statistically non-significant spatial autocorrelation (Moran's I = 0.06, $p = 0.088$).

Positive and negative changes in damage exhibited comparable levels of spatial autocorrelation, although decreases in damage tended to show slightly stronger clustering than increases. This pattern suggests that recovery processes may be somewhat more synchronized among neighboring locations than damage accumulation.

The observed contrast indicates that damage severity and annual damage changes differed substantially in their spatial structure. While damage severity exhibited consistent spatial clustering throughout the monitoring period, year-to-year changes in damage showed only weak spatial autocorrelation.

Taken together, these results indicate that damage severity exhibited substantially stronger spatial autocorrelation than year-to-year changes in damage. While Moran's I values for damage severity remained consistently positive throughout the study period, spatial autocorrelation of annual damage changes was generally weak.

4. Discussion

4.1. Damage Persistence and Recovery Processes

The coexistence of persistence and declining damage severity suggests that damage dynamics result from the interaction between continuing herbivore pressure and processes that reduce observed damage levels through time. Although damage levels showed substantial temporal continuity, the long-term decline in severe damage indicates that recovery mechanisms were sufficiently strong to prevent progressive accumulation of damage across the monitoring period.

Such patterns are consistent with observations from other forest ecosystems, where herbivore damage often persists across years but remains moderated by physiological recovery, compensatory growth, and variation in herbivore pressure among years [25,26].

The relatively frequent transitions toward lower damage classes observed in alder may also be related to its deciduous growth strategy. Unlike evergreen species that retain photosynthetically active foliage for multiple years, deciduous trees produce a new leaf cohort each growing season. Consequently, insect damage to leaves does not persist directly between years, potentially facilitating recovery from defoliation. Previous studies have suggested that plant recovery from herbivory depends strongly on plant life-history traits, resource availability, and compensatory responses, which may differ substantially among species and growth forms [27,28]. Therefore, the recovery patterns observed in alder stands may not necessarily be representative of tree species characterized by persistent foliage and greater potential for cumulative effects of herbivory over multiple years.

Importantly, persistence of damage should not be interpreted as irreversible deterioration. The transition analyses demonstrate that recovery remains a common outcome even under conditions of repeated infestation. Consequently, long-term trajectories of ecological impact emerge from the interaction between damage carry-over effects and compensatory recovery processes operating through time.

4.2. Patterns Consistent with Delayed Density-Dependent Regulation

The observed patterns are consistent with delayed density-dependent regulation, a mechanism widely reported in herbivorous insect populations and forest defoliator systems [29,30]. In such systems, ecological processes initiated during periods of high herbivore activity can influence subsequent levels of damage, creating stabilizing feedbacks that prevent the indefinite accumulation of ecological impact.

Several non-exclusive mechanisms may explain the patterns observed in alder stands. Increased herbivore activity may promote stronger regulation by predators and parasitoids, whose populations frequently respond positively to elevated prey abundance [9,12]. Similarly, pathogen transmission often becomes more effective at higher host densities, potentially reducing herbivore performance during subsequent years [31,32].

The negative association between previous infestation intensity and subsequent damage severity is consistent with the possibility of delayed density-dependent processes operating within the studied system.

Host-mediated processes may provide an additional explanation. Repeated herbivory can induce physiological and biochemical responses that reduce the suitability of host tissues for future feeding [2,13]. Experimental studies have demonstrated that induced plant defenses may persist long after the initial damage event and influence subsequent herbivore performance through changes in resource quality and host resistance [10,15].

Regardless of the underlying mechanism, the observed feedback structure suggests that ecological impact may not be determined solely by current infestation intensity. The observed pattern is also consistent with a forest health framework in which repeated herbivore pressure is counterbalanced by recovery processes operating at the tree and stand levels, thereby reducing the risk of persistent damage accumulation. Instead, damage dynamics appear to be influenced by processes operating across multiple years, producing a stabilizing effect that limits sustained accumulation of severe damage.

4.3. Relationship Between Occurrence and Damage Severity

One of the most important outcomes of the present study was the identification of both correspondence and divergence between infestation prevalence and damage severity. Although the two variables tracked each other closely at the broad temporal scale, they responded differently during the post-outbreak phase. Following peak infestation, damage severity declined faster than infestation prevalence, indicating that recovery mechanisms reduced realized ecological impact more rapidly than they reduced the spatial extent

of herbivore occurrence. This finding suggests that changes in ecological consequences cannot be inferred directly from occurrence metrics alone. The occurrence model further demonstrated that previous damage levels contributed little additional information once occurrence persistence had been accounted for. Together, these results indicate that prevalence and damage severity capture different dimensions of herbivore dynamics and should therefore be interpreted as complementary rather than interchangeable indicators.

Similar distinctions between occurrence-based and impact-based measures have been reported in other ecological systems, where population presence and ecological consequences respond differently to biological regulation and environmental conditions [16,33]. Likewise, long-term studies of forest herbivores indicate that population persistence and ecological impact may be influenced by partially independent processes [34,35].

Consequently, occurrence and damage severity should not be regarded as interchangeable indicators. Occupancy primarily reflects the spatial extent and persistence of herbivore populations, whereas damage severity reflects the realized impact of those populations on host trees. Together, these results indicate that ecological impact remains closely coupled to occurrence at broad temporal scales but exhibits stronger recovery and regulatory responses following periods of elevated infestation.

4.4. Spatial Structure of Damage Dynamics

Spatial analyses revealed a clear difference between the geographical patterns of damage severity and those of annual damage change. Mean damage severity remained spatially clustered throughout the monitoring period, indicating that locations characterized by relatively high or low damage levels tended to retain their position within the regional damage gradient over multiple years.

The interpolated maps further demonstrated that areas of elevated damage were not distributed randomly across the country. Instead, broad regional patterns remained visible throughout the study period, although their intensity varied among years.

By contrast, changes in damage severity between consecutive years exhibited only weak spatial autocorrelation. Local increases and decreases in damage were therefore only weakly synchronized among neighbouring monitoring plots, despite the persistence of larger-scale spatial patterns in damage severity itself.

This contrast suggests that the processes responsible for maintaining long-term differences in damage levels among regions may differ from those associated with short-term fluctuations. While geographical variation in damage severity remained relatively stable through time, annual changes in damage showed much greater local variability and limited spatial coordination.

Taken together, these results indicate that long-term spatial patterns were considerably more stable than annual damage dynamics. Consequently, the geographical distribution of damage severity appeared to be characterized by persistent regional structure, whereas year-to-year changes were dominated by local variation.

4.5. Implications for Forest Monitoring and Management

The strong year-to-year continuity of damage severity underscores the importance of repeated observations in forest health assessments. The results demonstrate that damage recorded in a given year is strongly influenced by previous damage history, suggesting that long-term monitoring provides substantially more information than isolated annual surveys.

Second, the results demonstrate that occupancy and damage severity provide complementary information about herbivore dynamics. Occupancy captures the extent and persistence of infestation, whereas damage severity reflects ecological consequences for

host trees. Because these indicators respond differently to recovery processes and delayed regulatory feedback, monitoring only one variable may provide an incomplete picture of forest health dynamics.

Third, the evidence for delayed density-dependent regulation suggests that periods of elevated infestation do not necessarily translate into continuously increasing ecological impact. Instead, compensatory mechanisms appear capable of reducing damage severity following periods of intense herbivore pressure. Consequently, management decisions should consider both current damage levels and recent infestation history when evaluating future risk.

More generally, the results highlight the importance of distinguishing between the presence of herbivorous insects and their ecological effects. Simultaneous monitoring of occurrence and damage severity may substantially improve interpretation of long-term forest condition assessments and provide a more complete understanding of herbivore impacts on forest ecosystems.

4.6. Study Limitations

Several limitations should be considered when interpreting the results of this study.

First, damage severity was assessed using ordinal field categories rather than direct quantitative measurements of leaf area loss. Although the ICP Forests protocol provides a standardized and widely used assessment framework, ordinal classes inevitably simplify continuous variation in herbivore damage. Consequently, the analyses should be interpreted as describing long-term patterns in observed ecological impact rather than precise estimates of defoliation intensity. Furthermore, damage severity was used as an indicator of observed herbivory intensity rather than a direct measure of tree performance. Consequently, the results should not be interpreted as evidence of impacts on growth, reproduction, survival, or overall fitness of host trees.

Second, insect occurrence was recorded as the presence of insect-induced damage rather than as direct measurements of herbivore abundance. Occupancy therefore represents an index of infestation extent and may not fully capture variation in local population density.

Third, the monitoring protocol does not allow identification of the relative contribution of individual herbivore species. Although alder leaf beetles are considered the most important folivorous insects associated with alder stands in Poland, the observed damage patterns likely reflect the combined effects of several herbivore taxa.

Fourth, the analyses focused primarily on temporal and spatial patterns of herbivore impact and did not explicitly incorporate climatic variables, hydrological conditions, stand structure, or natural enemy communities. These factors may contribute to the observed spatial heterogeneity and density-dependent responses.

In addition, occupancy and damage severity were derived from the same field observations of insect-induced damage. Consequently, the observed relationship between these variables should not be interpreted as a relationship between fully independent measures. Rather, occupancy and damage severity represent complementary descriptors of herbivory, capturing its extent and intensity, respectively. Therefore, part of the observed correlation between the two indicators may reflect their common observational basis.

Although several observed patterns were consistent with delayed density-dependent regulation, the monitoring data do not permit direct identification of the demographic or ecological mechanisms responsible for these relationships.

Although temporal dependence was addressed through lagged predictors and spatial structure was evaluated explicitly using Moran's I analyses, more complex hierarchical ap-

proaches such as mixed-effects or state-space models could provide additional insight into residual dependence associated with repeated observations of the same monitoring plots.

Furthermore, transitions from higher to lower damage classes should be interpreted as reductions in observed foliar damage rather than direct evidence of physiological recovery of host trees.

Finally, the observational nature of the dataset allows the identification of statistical associations and regulatory patterns, but does not permit direct inference regarding the ecological mechanisms responsible for delayed density-dependent feedback. Experimental studies will be required to distinguish among potential explanations, including host-mediated resistance, natural enemy regulation, and other density-dependent processes.

5. Conclusions

Our results show that long-term insect-induced damage in alder stands is characterized by substantial temporal persistence, frequent transitions toward lower damage classes, and a negative association between previous infestation intensity and subsequent damage severity. Although damage severity exhibited considerable temporal continuity, transitions toward lower damage classes were more frequent than transitions toward higher classes, contributing to a gradual decline in severe damage over the monitoring period.

Damage severity and insect occurrence followed similar long-term trajectories, but differed in their subsequent dynamics. In particular, damage severity declined more rapidly following periods of elevated infestation, indicating that observed damage levels were not fully explained by occurrence patterns alone.

The strong spatial structure of damage severity contrasted with the weak spatial autocorrelation of annual damage changes, suggesting that long-term patterns are associated with persistent site differences, whereas short-term dynamics are primarily local.

These patterns are consistent with the operation of ecological processes such as host responses, natural-enemy effects, or delayed density-dependent feedback. However, the observational nature of the monitoring data does not allow direct identification of the mechanisms responsible for the observed dynamics.

Overall, the study highlights the value of jointly assessing insect occurrence and damage severity in long-term forest monitoring programmes. These indicators provide complementary information on herbivore activity and associated damage patterns, thereby improving interpretation of forest condition assessments.

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