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Research article



A 30-year population decline of a threatened forest orchid associated with old growth forests

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ABSTRACT

Intensive forestry practices have transformed boreal forest landscapes, with profound consequences for biodiversity. Species dependent on old-growth forest characteristics are particularly vulnerable to habitat loss and structural simplification. We analyzed population trends and habitat preferences of the red listed and legally protected orchid *Goodyera repens* using 30 years (1993–2022) of data from the Swedish National Forest Inventory, examining occurrence, colonization, and extinction probabilities in relation to stand characteristics. *Goodyera repens* declined dramatically over the study period, with occurrence probability decreasing from 1.9% in 1993–1997 to 0.6% in 2018–2022—a 66% decline. Occurrence probability increased strongly with basal area, stand age, and moss species richness, with basal area emerging as the strongest predictor across all models. The species exhibited a very low colonization rate (0.7% over 10 years) combined with high local extinction risk (75.2%), with extinction probability increasing sharply when basal area declined between surveys (e.g. due to clear-cutting). This reflects the fundamental mismatch between the species' requirements for old-growth forest conditions and modern forestry operating on 60–100 year rotations that prevent forests from developing old-growth characteristics. The 66% decline documented here is most likely a direct consequence of forestry practices that systematically remove old-growth habitat by harvesting forests at the stage when they become suitable for the species. Without fundamental changes to forest management that allow forests to develop and maintain old-growth conditions across the landscape, *G. repens* and other old-growth specialists will continue to decline toward potential regional extinctions in coming decades.

1. Introduction

Global biodiversity loss continues at an unprecedented rate, with habitat degradation and land-use changes serving as primary drivers of ecosystem disruption and species extinctions (IPBES, 2019; Maxwell et al., 2016). Forest ecosystems, which harbor approximately 80% of terrestrial biodiversity, are particularly affected by anthropogenic activities, with intensive forestry practices homogenizing once-heterogeneous landscapes into structurally uniform stands (FAO, 2020). These large-scale anthropogenic activities affect boreal forests, which represent nearly one-third of global forest cover and provide essential ecosystem services, including climate regulation, carbon sequestration, and biodiversity maintenance (Gauthier et al., 2015; Bradshaw et al., 2009). The simplification of the forests also results in altered microclimatic conditions and diminished refuges for species sensitive to environmental change (Gustafsson and Perhans, 2010; Halpern, 1989; Heithecker and Halpern, 2007).

In Fennoscandia, intensive forestry practices have led to significant declines in old-growth forests and associated biodiversity (Kouki et al., 2001; Kuuluvainen et al., 2015). In Sweden, where production forestry dominates the landscape and constitutes a major component of the national economy, more than 10% of forest-associated species are now red-listed, with many populations declining and becoming increasingly fragmented (Hansen et al., 2013). Previous studies have consistently documented the negative effects of logging across various taxonomic groups, including vascular plants, bryophytes, lichens, and fungi (Hylander and Weibull, 2012; Johansson et al., 2018; Dahlberg et al., 2001; Lõhmus and Kull, 2011). Species that rely on the stable microclimatic conditions and structural complexity of old-growth forests are particularly vulnerable to habitat loss and fragmentation (Åström et al., 2007). Among these old-growth specialists, orchids represent a particularly sensitive group, characterized by their dependence on specific habitat conditions, symbiotic mycorrhizal associations, and intolerance to disturbance (Lõhmus and Kull, 2011; Haeussler et al., 2002).

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One example of such an orchid species is *Goodyera repens*, which is associated with late-successional forests with high habitat heterogeneity (Widenfalk and Weslien, 2009; Johansson et al., 2025). The species is sensitive to habitat alterations, thriving primarily in undisturbed old-growth forests characterized by stable environmental conditions and complex structural features (Lõhmus and Kull, 2011). The species is known to experience local extinctions following clear-cutting operations, and the short rotation cycles employed in managed forests further restrict its establishment and long-term persistence (Johnson, 2014; Johansson et al., 2025). In Sweden, this species is afforded legal protection under the Species Protection Ordinance (Artskyddsförordning 2007:845). Despite this protection and its status as a vulnerable species on the Swedish Red List (VU, SLU ArtDatabanken, 2020), there remains a significant knowledge gap regarding its population trend, colonization-extinction dynamics, and specific habitat preferences. Understanding the drivers of colonization and extinction for old-growth dependent species is critical for conservation planning, yet long-term demographic data linking habitat conditions to population dynamics remain scarce. Such knowledge is essential for developing forest management strategies that balance timber production with biodiversity conservation. *Goodyera repens* serves as a valuable model species in this context: its sensitivity to forest management and association with old-growth characteristics make it representative of a broader suite of species threatened by modern forestry practices across the boreal biome.

This study aims to enhance our understanding of *G. repens* habitat preferences and population dynamics within the context of managed boreal forests. We utilise data from the Swedish National Forest Inventory (NFI), where the species has been recorded since 1993. Specifically, we analyze its population trends (occurrence probability over time) over the last 30 years, and its occurrence, local extinction, and colonization probability in relation to detailed habitat factors.

2. Methods

2.1. Study species

Goodyera repens (L.) R. Br. is a small evergreen orchid (Orchidaceae) with a circumpolar distribution spanning the boreal and hemiboreal zones of Europe, Asia, and North America (Fig. 1). The species exhibits both vegetative spread via rhizomes and sexual reproduction through wind-dispersed seeds, and requires obligate mycorrhizal associations for successful germination and early establishment (Cameron et al., 2006). Across its range, *G. repens* is characteristically associated with late-successional coniferous forests displaying old-growth characteristics (Widenfalk and Weslien, 2009; Lõhmus and Kull, 2011; Johnson, 2014).

In Sweden, the species is classified as Vulnerable (VU) on the national Red List (SLU ArtDatabanken, 2020). Legal protection under Sweden's Species Protection Ordinance (SFS 2007:845) prohibits intentional damage or removal of individuals, with enforcement occasionally resulting in the suspension of forestry operations where populations occur. This regulatory role has generated considerable discussion within the forestry sector, yet fundamental questions regarding the species' specific habitat requirements, colonization-extinction dynamics, and population trend remain inadequately addressed.

2.2. Study area and data

To analyze the occurrence and population dynamics of *G. repens*, we used data from the Swedish National Forest Inventory (NFI, Fridman et al., 2014). The NFI divides Sweden into five geographical regions; we used data from regions 2, 3, and 4 (called North, Mid and South in Fig. 1), which encompass the primary distribution range of *G. repens* in Sweden. We restricted our analysis to productive forest land, which is defined by soil productivity (potential for forest growth) regardless of management status, and thus includes both managed forests and protected areas. This land category represents the most suitable habitat for *G. repens* and is subject to more comprehensive data collection compared to other land types. Our analysis included only data from permanent circular plots (with 10 m radius) collected between 1993 and 2023, the period during which *G. repens* has been systematically inventoried. This resulted in 12,147 plots in total with basal area weighted forest age ranging 1–290 years (median = 47, 25th percentile = 24, 75th percentile = 89). The average time between surveys in the same plot was 10 years, resulting in three visits for most of the plots over the entire study period (Fridman et al., 2014).

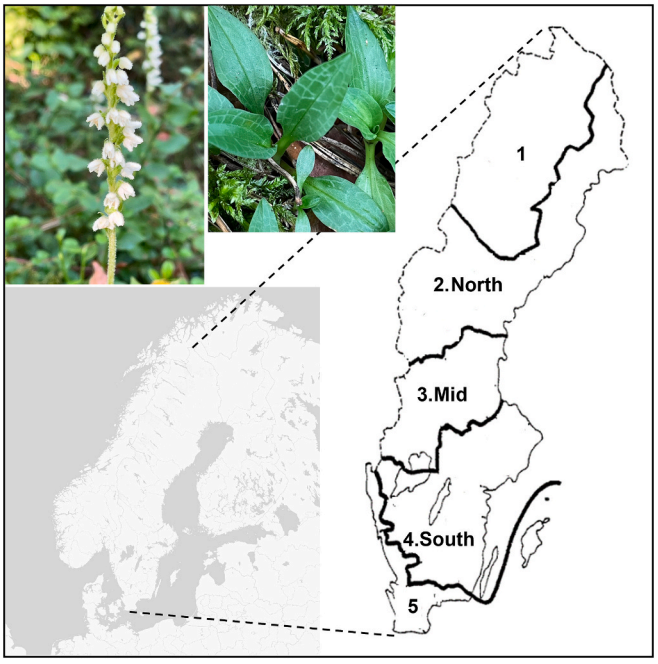

Fig. 1. Sweden divided into geographical regions where regions 2, 3, and 4 (here called North, Mid, and South) were used as study areas because they cover the main distribution of *Goodyera repens* (inset photos show the evergreen leaf rosettes and flowering inflorescences).

Given the extensive data collected during the NFI, we selected variables considered most relevant to our study (Table 1). Peat coverage, moving soil water, soil depth, bottom layer, field layer, and even-agedness were processed to reduce the number of categories (for details see Table A1, Appendix A, Supplementary material). Proportion of pine and spruce and the number of tree, moss, and herb species were calculated from the original data (Table A1). For the colonization and extinction analyses we also calculated the decrease in basal area and time between surveys (Table A1).

2.3. Statistical analysis

To analyze the population trend of *G. repens* over the study period, we used a generalized linear model (GLM) with binomial distribution, where the occurrence (presence/absence) of *G. repens* was the response variable and survey year the explanatory variable (mean-centered and standardized). To assess overall regional differences in occupancy, we used the same type of model but with region as a factorial explanatory variable. These two analyses used all available occurrence data (n = 29,356 observations).

For subsequent analyses of occurrence probability and colonization-extinction dynamics, the dataset was reduced due to missing values in explanatory variables at some sites, resulting in 28,405 observations. We used generalized linear mixed models (GLMMs) with binomial error distribution and logit link function to identify predictors of (1) occurrence probability, (2) colonization, and (3) extinction. For occurrence

Table 1
Variables from the Swedish National Forest Inventory used for modelling occurrence probability and population dynamics of *Goodyera repens*. Several variables were processed to reduce the number of categories or to create new variables; details on how these processed variables were derived are provided in Table A1.

Variable	Type (unit)	Categories or range	Original or processed
Plot ID			Original
Year of inventory	Continuous (year)	1993–2022	Original
Region	Categorical	2, 3, 4	Original
Presence of peat	Categorical	0: no peat 1: peat is present	Processed
Moving soil water	Categorical	0: never or rarely 1: shorter or longer periods	Processed
Soil type	Categorical	0: no moraine 1: moraine	Processed
Soil depth	Categorical	0: shallow 1: deep	Processed
Bottom layer	Categorical	1: lichen type 2: wetland moss type 3: mesic moss type	Processed
Field layer	Categorical	0: no bilberry (other) 1: bilberry	Processed
Ground inclination	Continuous (%)	2.5–70	Original
Basal-area weighted mean height	Continuous (m)	0.1–37.5	Original
Basal-area weighted stand age	Continuous (years)	1–290	Original
Basal area (total)	Continuous (m^2/ha)	0–69	Original
Basal-area weighted mean stem diameter	Continuous (mm)	0, 846	Original
Even-agedness	Categorical	0: not even aged 1: more or less even aged	Processed
Gaps	Categorical	0: maximum of one gap 1: 2–3 gaps 2: minimum of 4 gaps	Original
Proportion of pine and spruce	Categorical	0: <50% 1: ≥50%	Processed
Soil moisture	Categorical	1: dry 2: mesic 3: mesic-moist 4: moist 5: wet	Original
Number of tree species	Continuous (count)	0–7	Processed
Number of moss species	Continuous (count)	0–3	Processed
Number of herb species	Continuous (count)	0–9	Processed
Basal area decrease[a]	Continuous	−40.3–63.9	Processed
Time between surveys[a]	Continuous	9–25	Processed

[a] Only used for colonization and extinction models.

probability models, all models included survey year ($n = 30$), region ($n = 3$), and plot identity ($n = 11{,}961$) as random intercepts to account for temporal, spatial, and site-level non-independence. Random slopes for survey year within plots were tested but failed to converge due to data sparsity. For colonization and extinction models, site identity was excluded due to sparse data (maximum two observations per site) and model convergence issues; these models included only survey year and region as random intercepts.

We employed a two-stage model selection approach for all three model types. First, we screened candidate predictors individually against a null model containing only random effects. For occurrence models, the screening for candidate predictors included all stand characteristics measured at the time of survey. For colonization and extinction models, we also added change in basal area and time between surveys. Predictors that improved AIC relative to the null model were retained for multivariate modelling. Second, we performed manual backward stepwise selection on multivariate models, iteratively removing predictors and retaining only those whose removal decreased AIC by >2 units (Burnham and Anderson, 2002). Continuous predictors were scaled (mean-centered and standardized) prior to analysis to facilitate model convergence and coefficient interpretation. We examined pairwise correlations between predictors; while moderate correlations were observed among forest structure variables (the highest $r = 0.6$ between basal area and mean tree diameter), all variance inflation factors (VIF) remained below 1.6. These low VIF values indicate that multicollinearity did not destabilize the model estimates. Statistical significance for individual predictors was evaluated at $\alpha = 0.05$.

As a complement to the analyses of *Goodyera repens*, we also assessed trends in basal area (the sum of cross-sectional stem areas per hectare) and the proportion of old forest (>80 years) over the study period using generalized linear models with year as a continuous predictor (mean-centered and standardized). Basal area was modelled with a Gaussian distribution, while old forest occurrence (binary: >80 years or not) was modelled with a binomial distribution. All models were fitted using the glmmTMB package (Brooks et al., 2017) in R version 4.2.2 (R Core Team 2024).

3. Results

3.1. Population trend and regional differences

The dataset from the NFI consisted of 29,356 separate inventories from 12,147 permanent plots between 1993 and 2022. *Goodyera repens* was observed in 331 inventories (1.13%) and was present in 264 plots (2.17%). The occurrence probability of *G. repens* showed a significant decrease over time ($\beta = -0.24$, $z = -4.26$, $p < 0.001$; Fig. 2). During the first five years (1993–1997), the mean proportion of occupied plots was 0.019 (SE = 0.0022), compared to 0.006 (SE = 0.0017) during the last five years (2018–2022), indicating a 66% decline over the entire study period. The average decline in individual plots was 35.0% between the first and the last survey, representing an average interval of 20 years. The occurrence probability of *G. repens* was lowest in the southernmost

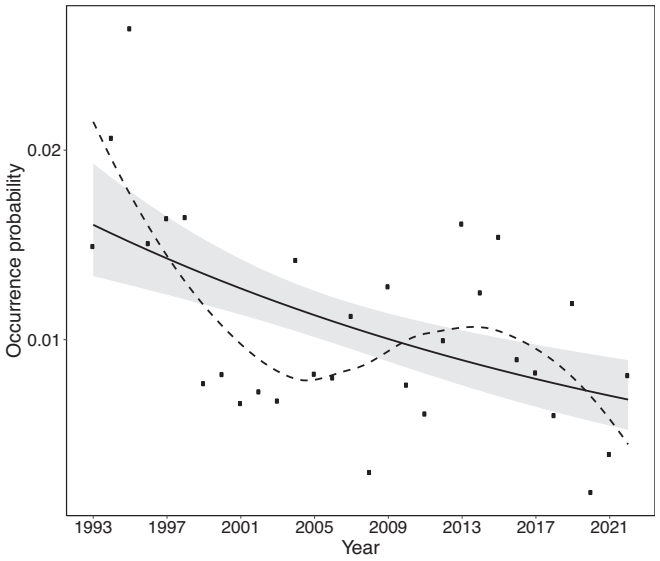

Fig. 2. The occurrence probability of *Goodyera repens* over time (1993 to 2022) based on data from the Swedish national forest inventory. Points show the occupancy per year, whole line with 95% confidence intervals (grey) show model predictions, and broken line a Loess smoothing line.

region included in the study (Fig. 3), but was only significantly lower compared to the mid region.

3.2. Occurrence probability

After removing rows with missing values for any explanatory variable, the dataset was reduced to 28,405 inventories from 11,961 permanent plots. *Goodyera repens* was observed 328 times (1.15% of inventories) and was present in 261 plots (2.18%).

The occurrence probability of *G. repens* increased with increasing basal area (Fig. 4), stand age, and number of moss species (Table 2). It was also higher in conifer-dominated plots and plots with canopy gaps (Table 2). Based on the change in AIC when removing each variable from the final model (ΔAIC), basal area was the most important predictor of occurrence, followed by number of moss species and stand age (Table 2).

3.3. Colonization and extinction dynamics

Of 206 plots where *Goodyera repens* was present at the first inventory, it went extinct in 155 plots, representing a 75.2% local extinction risk over approximately 10 years. Of 16,238 plots where the species was initially absent, colonization occurred in 114 plots, representing a 0.7% local colonization probability.

The extinction probability of *G. repens* increased with decreasing basal area between surveys and time since the last survey (Table 3), and was lower in plots with bilberry in the field layer. Decreasing basal area was by far the strongest predictor based on ΔAIC (Table 3).

Colonization probability increased with increasing basal area, stand age, tree species richness, moss species richness, and herb species richness (Table 4). It was higher in plots with bilberry in the field layer, moraine soil type, and even-aged stands, but lower on deep soils and in plots with multiple canopy gaps. The strongest predictors of colonization were basal area decrease (ΔAIC = 50.0), baseline basal area (ΔAIC = 45.5), and stand age (ΔAIC = 37.1; Table 4).

3.4. Changes in basal area and proportion of old forest

Basal area increased significantly over the study period (β = 0.55, SE = 0.07, t = 7.55, p < 0.001). Mean basal area increased from approximately 17.3 m^2/ha in 1993 to 21.2 m^2/ha in 2022, an increase of roughly 23% over the study period.

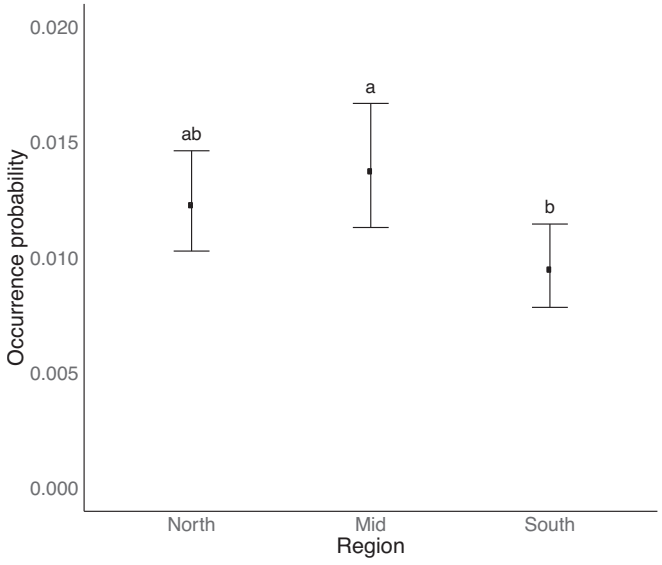

Fig. 3. The occurrence probability in relation to region. Letters signify statistical differences.

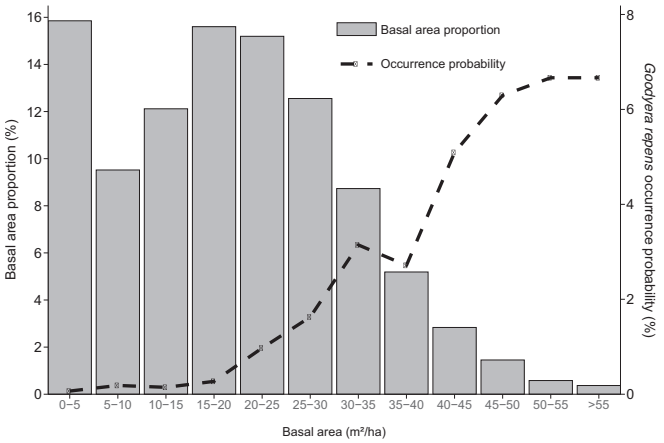

Fig. 4. Distribution of basal area across plots (grey bars, left y-axis) and occurrence probability of *Goodyera repens* across basal area classes (dashed line, right y-axis), based on 28,405 inventories (n = 28,405) from 11,961 permanent plots. Note the different scales on the two y-axes.

Table 2
Parameter estimates (with SE) and p-values from the final model of *Goodyera repens* occurrence probability. ΔAIC = the increase in AIC when removing the variable from the final model. Region, year, and plot ID were included as random effects.

Variable	Estimate (SE)	p-value	ΔAIC
Basal area	1.794 (0.21)	<0.001	93.5
Number of moss species	1.241 (0.25)	<0.001	27.6
Stand age	0.716 (0.21)	<0.001	9.6
Conifer dominated	3.560 (1.89)	0.060	3.9
Canopy gaps (2–3 gaps)	0.803 (0.31)	0.010	3.9
(>3 gaps)	0.831 (0.43)	0.054	

Table 3
Parameter estimates, standard errors, and p-values from the final generalized linear mixed model testing extinction probability of *G. repens*. ΔAIC shows the increase in AIC when removing each variable. Year and region were included as random effects.

Variable	Estimate	Std. Error	p-value	ΔAIC
Basal area decrease	1.438	0.391	<0.001	22.0
Time between surveys	1.287	0.737	0.081	4.1
Field layer (bilberry)	−0.903	0.474	0.057	2.0

Table 4
Parameter estimates, standard errors, and p-values from the final generalized linear mixed model testing colonization probability of *G. repens*. ΔAIC shows the increase in AIC when removing each variable. Year and region were included as random effects.

Variable	Estimate	Std. Error	p-value	ΔAIC
Basal area decrease	−0.847	0.155	<0.001	50.0
Basal area	0.820	0.116	<0.001	45.5
Stand age	0.762	0.118	<0.001	37.1
Species richness of trees	0.385	0.103	<0.001	11.9
Number of moss species	0.424	0.129	0.001	9.5
Canopy gaps (2–3 gaps)	−0.809	0.263	0.002	9.3
(>3 gaps)	−0.797	0.373	0.032	
Species richness of herbs	0.294	0.088	0.001	9.0
Presence of bilberry (0/1)	0.563	0.218	0.010	5.0
Even-age (not even/even)	0.632	0.257	0.014	4.4
Soil type (not moraine/moraine)	0.582	0.264	0.028	3.4
Soil depth (shallow/deep)	−0.536	0.249	0.031	2.3

The proportion of old forest (>80 years) decreased significantly over

the study period ($\beta = -0.07$, SE = 0.01, $z = -5.62$, $p < 0.001$). The predicted proportion of plots classified as old forest declined from 33% in 1993 to 27% in 2022, a relative decrease of approximately 17%.

4. Discussion

We show that the threatened orchid *Goodyera repens* has declined by 66% in Swedish forests over the past three decades (1993–2022) based on monitoring data, a dramatic population loss consistent with broader declines of forest-dependent species across northern Europe (Kouki et al., 2001; Paillet et al., 2010; Kuuluvainen et al., 2015) and European orchids generally (Kull and Hutchings, 2006; Vogt-Schilb et al., 2015; Damgaard et al., 2020). This steep decline is concerning given the species' legal protection and red-list status, and seems connected to forestry history. Lower occurrence in southern Sweden likely reflects the region's longer history of intensive forest management, which began earlier and has resulted in fewer remaining old-growth forests compared to further north (Björklund, 1984; Östlund et al., 1997). This regional pattern illustrates how historical land-use legacies shape contemporary biodiversity patterns, with more intensively managed landscapes showing greater species losses (Kouki et al., 2001; Löfman and Kouki, 2001; Ericsson et al., 2005). Such legacy effects are well documented across other habitat types, where species with poor colonizing abilities remain restricted to sites with long habitat continuity, even centuries after land-use changes (Hermy et al., 1999; Kuussaari et al., 2009; Fagúndez, 2013).

Our analyses reveal that *G. repens* occurrence, colonization, and extinction are fundamentally linked to forest developmental stage and the suite of structural attributes that accumulate with stand age —a dependency shared by many old-growth specialists including saproxylic beetles, cryptogams, and wood-inhabiting fungi (Nordén et al., 2013; Gustafsson et al., 2024; Bergman et al., 2025). While basal area (or its change between surveys) emerged as the strongest predictor across all models—a positive relationship not previously reported for orchids in boreal forests—its importance likely operates through multiple interconnected pathways tied to forest succession. High basal area creates closed-canopy conditions that maintain stable humidity levels through reduced evapotranspiration and wind exposure (Vesala et al., 2005), while simultaneously reducing light availability and competitive dominance by light-demanding species, allowing shade-tolerant specialists to persist (Reich et al., 2012; Hekkala et al., 2023). Forests suitable for *G. repens* thus represent old-growth systems that have developed not only high stem density and canopy closure but also the structural heterogeneity (here for instance seen in tree diversity and canopy gaps), stable microclimates, diverse moss communities, and specialized mycorrhizal networks that define old-growth ecosystems. Although standing volume and basal area have increased in Swedish forests over the past century (Jacobsson et al., 2025), which is also seen in our results, this is the result of general densification (Kyaschenko et al., 2022) and does not compensate for the loss of old-growth characteristics that accumulate only with stand age. The correlations we observed between basal area, stand age, and moss species richness reflect their interdependence in forest ecosystems, where time allows the natural development of structural complexity and resource accumulation critical for biodiversity (Bergeron and Harper, 2009; Angelstam et al., 2011; Nordén et al., 2014; Johansson et al., 2025). As forests mature and basal area increases, the carpet-forming mosses develop into thick, stable mats that provide the specific microhabitat conditions where *G. repens* establishes and persists (Esseen et al., 1997; Hylander and Weibull, 2012). These moss layers do not simply co-occur with *G. repens* but likely facilitate it through multiple mechanisms—buffering rhizomes against temperature and moisture fluctuations, maintaining stable substrate conditions, and potentially harboring the mycorrhizal fungi essential for orchid establishment (Cameron et al., 2006; Varenius et al., 2016).

The observed population decline and the demographic crisis facing *G. repens*—combining extremely low colonization rates (0.7%) with high extinction risk (75.2% over 10 years)—reflects a mismatch between the species' habitat requirements and prevailing forest management. Modern forestry operates on 60–100 year rotations (Kuuluvainen et al., 2015) that prevent forests from reaching the structural maturity the species requires. Our results show that *G. repens* occurrence probability increases markedly in forests with basal area > 30 m^2/ha, which coincides with typical harvest thresholds in Swedish forestry (25–35 m^2/ha for commercially mature stands). This means that many forests are harvested at the developmental stage when they become suitable for *G. repens* establishment, creating a systematic barrier to colonization across the managed landscape. The landscape-scale transformation is evident in the dramatic shift in age-class distribution, with young production forests expanding while maturing forests decline (Bergman et al., 2025). This is also seen in our data: the proportion of old forest (>80 years) declined by 17% over the study period. This systematic replacement of maturing forests with young stands has profound consequences for biodiversity across multiple taxonomic groups (Bergman et al., 2025; Gustafsson et al., 2025). The significantly lower occurrence of *G. repens* in southern Sweden, where intensive management has the longest history (Björklund, 1984; Östlund et al., 1997), previews the trajectory for other regions as forestry intensification continues. The species' extremely low colonization rates likely reflect limited dispersal capacity (Brzosko et al., 2017) as dispersal sources are eliminated when old-growth forests decline in the surrounding landscape (Gustafsson et al., 2025). However, even when dispersal occurs, the decades required for forests to develop old-growth characteristics—high basal area, canopy closure, moss layer development, mycorrhizal networks, and microclimate stability (Moning and Müller, 2009; Nordén et al., 2014)—means that colonization cannot offset extinctions. The temporal mismatch between commercial rotation age and habitat maturity thus creates an extinction trap: forests are removed from the landscape just as they approach suitability for the species. Conversely, the high extinction rate when basal area is reduced reflects acute sensitivity to the cascading changes following canopy opening: altered light regimes, reduced humidity (Heithecker and Halpern, 2007), disrupted moss layers (Hylander and Weibull, 2012), and likely disruption of mycorrhizal partnerships (Varenius et al., 2016). These changes occur rapidly following timber harvest, whereas suitable habitat conditions accumulate slowly over many decades, creating a fundamental demographic asymmetry and an extinction debt (Kuuluvainen, 2009) where remaining populations disappear faster than new ones can establish.

4.1. Limitations

Several limitations should be acknowledged. First, occurrence probability reflects site occupancy rather than abundance; however, for a clonal, long-lived species with extremely low colonization rates, declining occupancy at this scale strongly indicates genuine population decline. Second, *G. repens* is small and potentially overlooked, and while NFI protocols have remained consistent, we cannot fully exclude variable detectability. Additionally, the small spatial scale of NFI plots may underestimate colonization, as the species could colonize stands outside plot boundaries. The magnitude and consistency of the decline nevertheless suggest a real population signal. Third, our analysis was restricted to productive forest land, which is defined by soil productivity and includes both managed forests and nature reserves. Other land categories where the species may also occur were not assessed. Fourth, the low colonization rate (0.7%) and limited number of initially occupied plots constrain statistical power, and these results should be interpreted as indicative rather than definitive. Fifth, colonization and extinction were analyzed separately rather than using dynamic occupancy models, which would better capture state-dependence but require repeated within-season visits not available in NFI data. Finally, while our findings strongly implicate forestry practices as the primary driver of decline, the correlative nature of observational data precludes definitive

causal inference.

4.2. Implications for conservation

Conservation of *G. repens*, as well as many other old-growth forest specialists, requires fundamentally rethinking forest management in areas where the species persists. First, maintaining high basal area and avoiding practices that substantially reduce stand density must be absolute priorities in occupied forests—the high extinction risk associated with basal area reduction (especially clear-cutting) leaves no margin for experimentation (Widenfalk and Weslien, 2009; Lõhmus and Kull, 2011). Second, protecting existing old-growth forests provides both refugia for current populations and dispersal sources for potential colonization (Lindenmayer et al., 2006), though the low colonization rates suggest even well-distributed old forests may not enable landscape-scale recovery on relevant timescales. Third, promoting extended rotations and retention forestry in the broader matrix (Gustafsson et al., 2012; Fedrowitz et al., 2014) could gradually expand the area of developing old-growth characteristics, though this represents a multi-generational commitment given the decades required for habitat maturation.

These recommendations align with broader boreal forest biodiversity conservation goals (Mori et al., 2017), as the habitat conditions supporting *G. repens* benefit numerous old-growth specialists (Paillet et al., 2010). The 66% decline documented here reflects the systematic removal of old-growth habitat through forestry practices that harvest forests at the stage when they become suitable for the species. These findings have implications beyond Fennoscandia, as boreal forests across Russia, Canada, and Alaska face similar pressures from intensifying forestry (Gauthier et al., 2015), and old-growth dependent species—including bryophytes, lichens, saproxylic insects, and cavity-nesting birds—may face analogous threats. Without fundamental changes to forest management that allow forests to develop and maintain old-growth conditions across the landscape, *G. repens* and other old-growth specialists face continued decline and potential regional extinctions in coming decades.

CRediT authorship contribution statement

Victor Johansson: Writing – original draft, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Matilda Jansson:** Writing – review & editing, Formal analysis, Data curation. **Karl-Olof Bergman:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Description of explanatory variables and their pair-wise correlations. Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.111765.

Data availability

The authors do not have permission to share data.

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