ORIGINAL RESEARCH

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Major disturbances test resilience at a long-term boreal forest monitoring site

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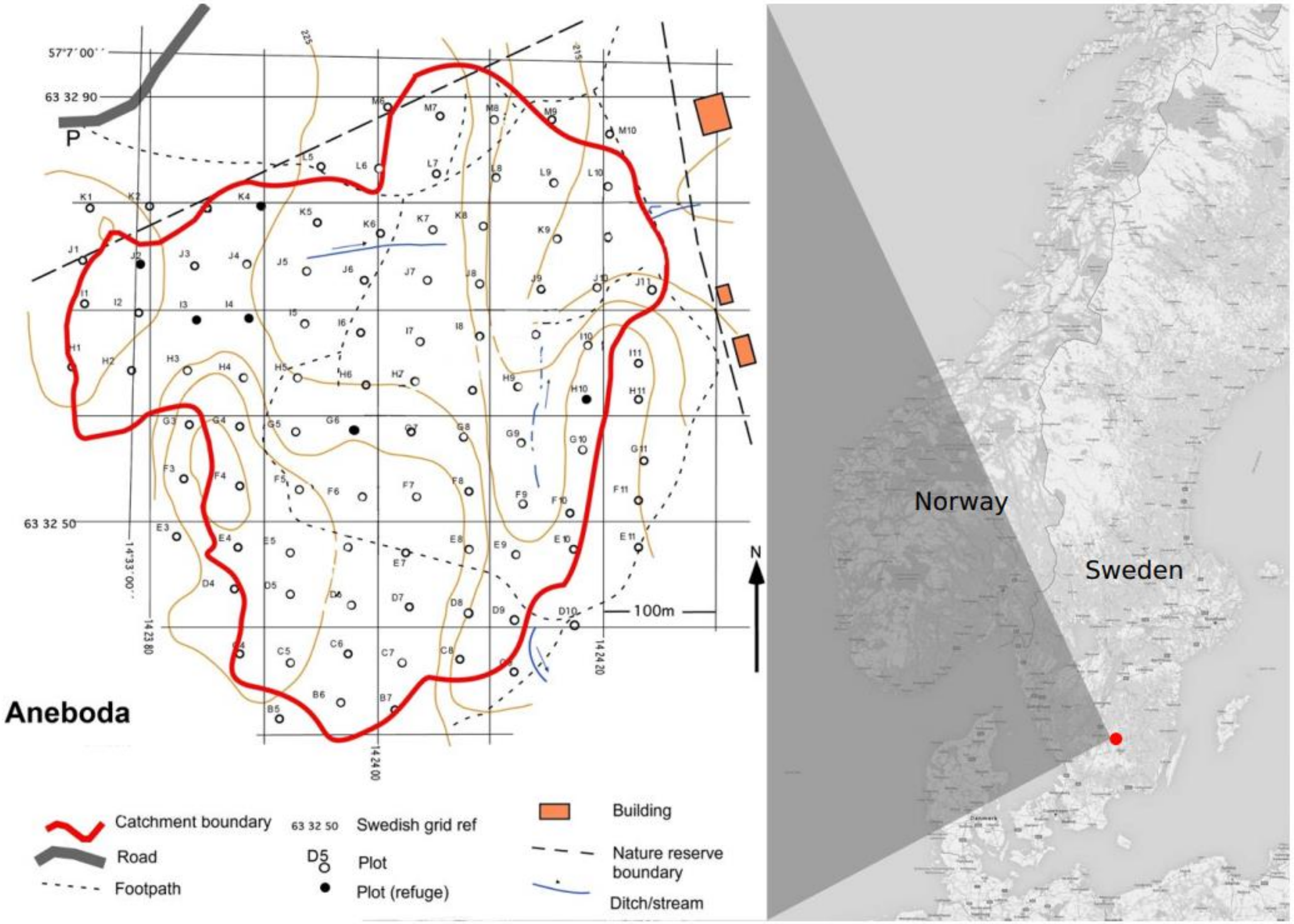

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Pulse disturbances
Bark beetle
Wind
N deposition, climate change
Long term press disturbances
Resilience?
Or regime shift?

- Aneboda site, southern Sweden, spruce forest
- Storm Gudrun in 2005 felled ca. 20% of trees
- Followed by bark beetle outbreak- by 2011 over 50% of trees >25cm DBH were dead
- Spatially heterogenous impact- refuge areas? Some plots retained cover of mature spruce.
- Shift to beech domination possible

Photos: Ulf Grandin

Questions

- How have vascular plant species abundances, taxonomic and functional diversity, and community composition changed in the post-disturbance period?

- Do changes show spatial and/or temporal patterns? Are “refuges” really refuges? Is there continuing change over time?

- Do changes show evidence of an ongoing regime shift to deciduous dominated state?

Results - changes in overall cover

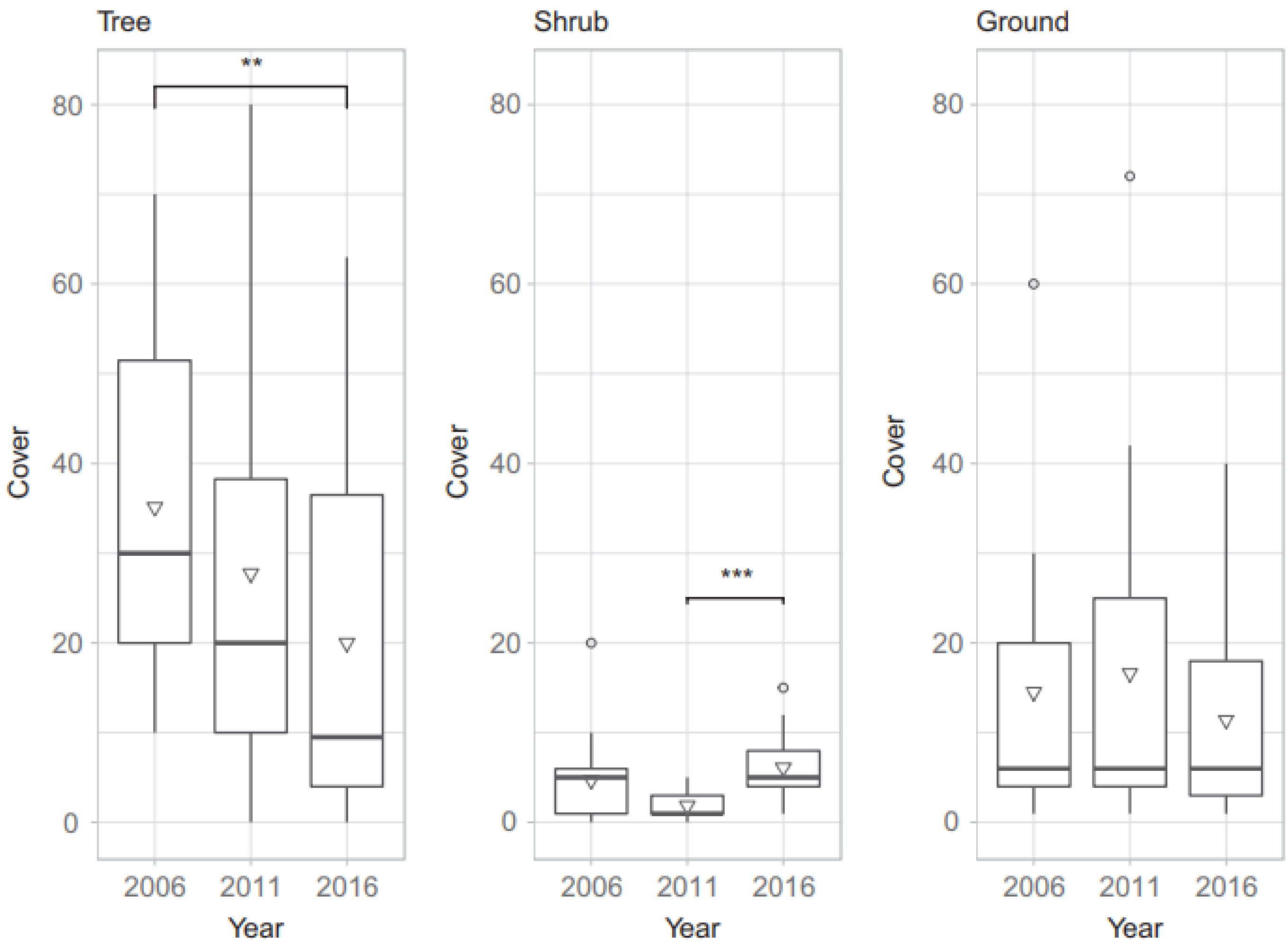

FIGURE 3 Between-year changes in mean cover by layer (across all sampled plots).Upper and lower limits of the box are 75th and 25th percentile, respectively, horizontal bars represents the median, and triangles show mean values. Whiskers extend up to 1.5 times the interquartile range. Outliers beyond that distance shown by open circles. Bars and asterisks indicate significance differences (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$)

Community composition – no change?

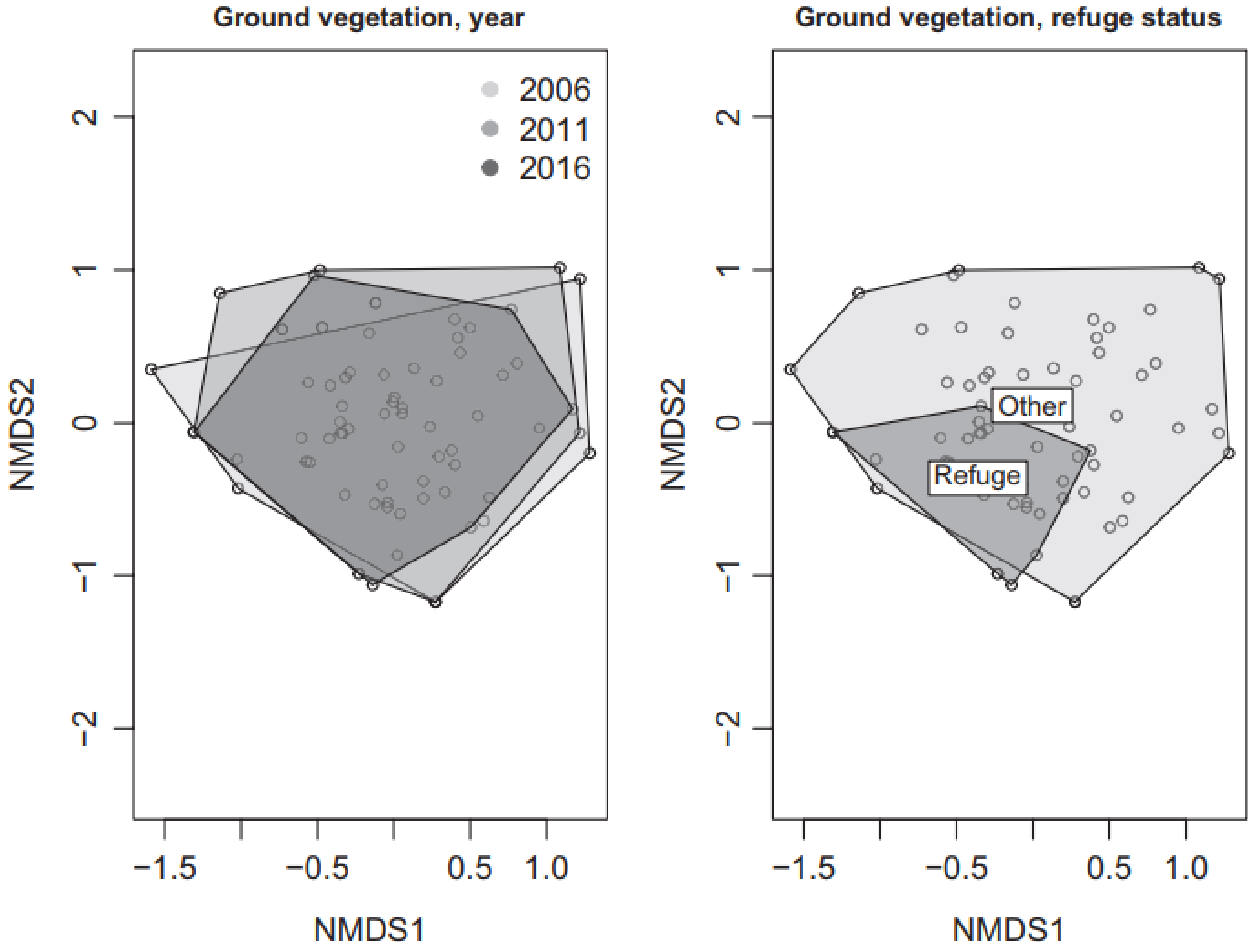

FIGURE 5 nMDS of ground layer vegetation plots showing convex hulls for survey years (left) and refuge status (right) shows considerable overlap. Convex hulls drawn from points representing plots, based on Bray–Curtis dissimilarity, stress 0.17

Community composition : divergence

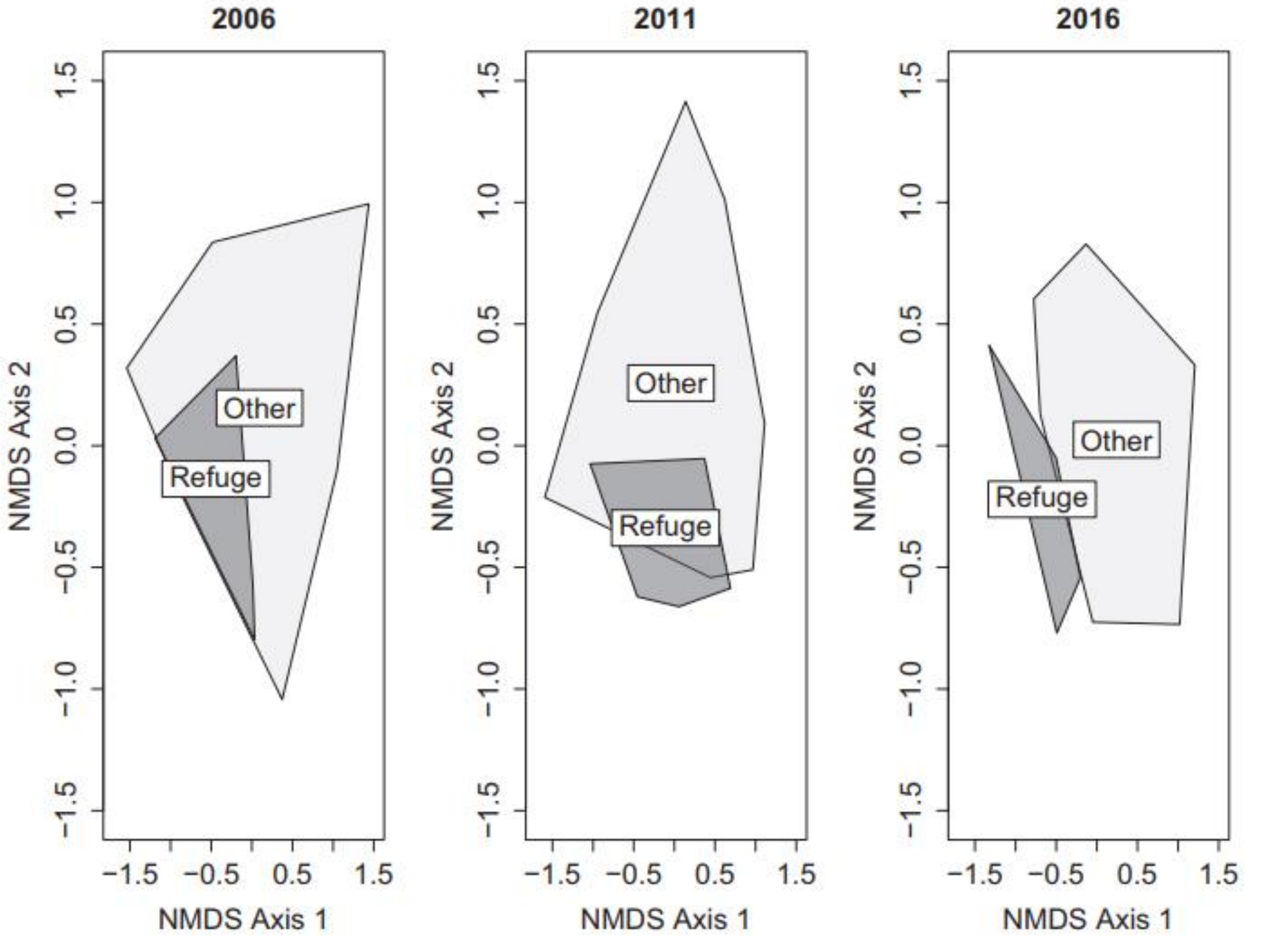

FIGURE 6 nMDS of ground layer plots with convex hulls indicating refuges and nonrefuges, showing an increasing separation of refuges and nonrefuges over time, convex hulls drawn from points representing plots, Bray–Curtis dissimilarity (stress 0.11, 0.12, 0.11)

Community composition : tests

TABLE 1 PERMANOVA and Betadisper test results for differences in community composition and multivariate dispersion, with year and refuge status as factors. Tests were performed on all plots together, and separately on refuges/nonrefuges only

	Permanova		Betadisper	
	Refuge	Year	Refuge	Year
Ground layer				
All plots	***	NS	***	NS
Refuges	na	NS	na	NS
Nonrefuges	na	*	na	NS
Shrub layer				
All plots	*	NS	NS	NS
Refuges	na	NS	na	NS
Nonrefuges	na	NS	na	NS
Tree layer				
All plots	**	*	***	*
Refuges	na	NS	na	NS
Nonrefuges	na	***	na	NS

Note. Asterisks indicate a significant result. "NS" indicates a nonsignificant result, "na" indicates test not performed for this combination of plots and factor.
*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

- Refuges differ from non-refuges in all vegetation layers
- There are changes over time in non-refuges (but not in refuges)

Taxonomic and functional diversity

	2006	2011	2016	Difference (ANOVA)
All plots	1.61 (0.47)	1.89 (0.44)	2.06 (0.46)	**
Refuges	1.78 (0.36)	1.78 (0.46)	1.61 (0.56)	NS
Nonrefuges	1.55 (0.50)	1.94 (0.44)	2.21 (0.30)	***

**$p < 0.01$; ***$p < 0.001$.

TABLE 4 Mean Shannon diversity index values by year and refuge status, standard deviations in brackets

TABLE 3 Changes in functional diversity indices (functional dispersion (FDis), evenness (FEve), and Rao's quadratic entropy [RaoQ]). Tested using ANOVA/Kruskal–Wallis with year as grouping)

	Functional evenness	Functional dispersion	Functional richness	Rao's Q
All plots	ns	*	ns	*
Refuges	ns	ns	ns	ns
Nonrefuges	ns	**	ns	**

*$p < 0.05$; **$p < 0.01$

Increases in both taxonomic and functional diversity, driven by the disturbed areas.

Which species are driving changes?

- Decreases in forest species
- Increases in ruderal species
- Increase in spruce

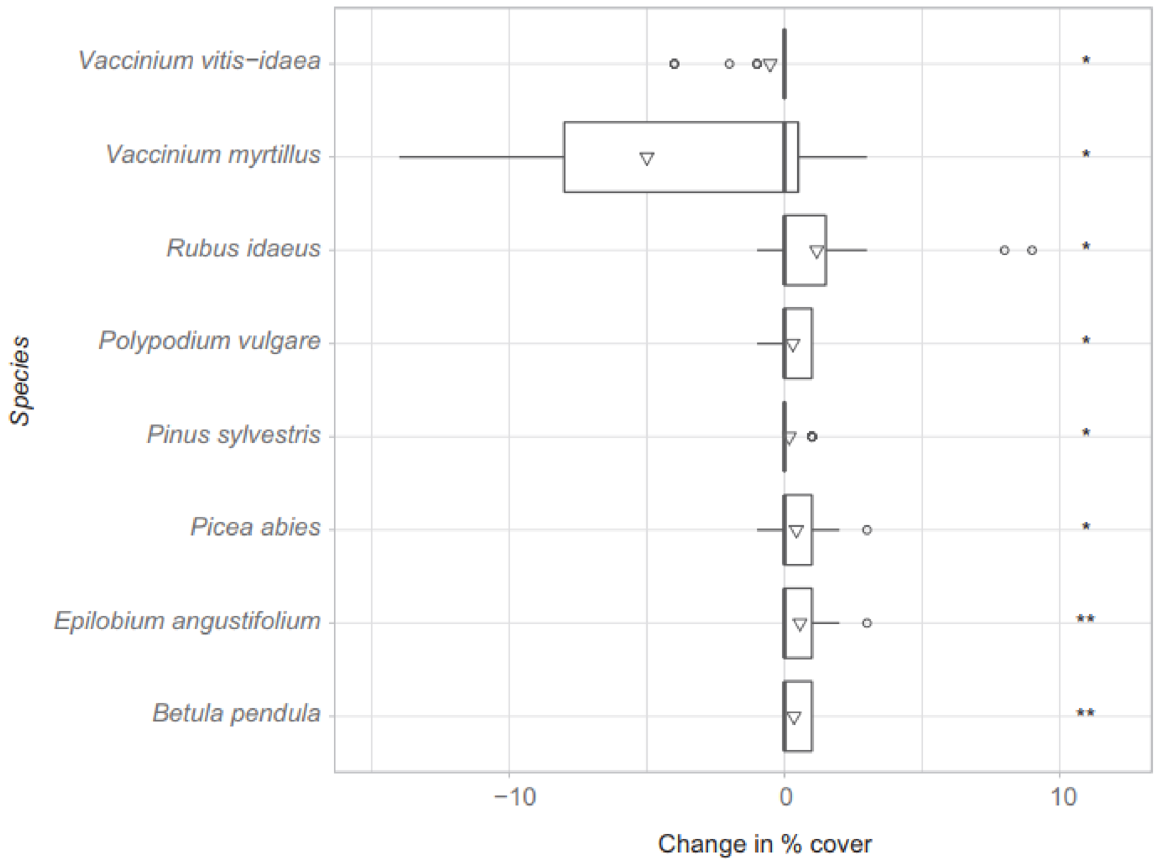

FIGURE 4 Significant changes in percentage cover of vascular plant species in the ground layer 2006–2016. Upper and lower limits of boxes are 75th and 25th percentile, respectively, vertical bars represent the median, and triangles show mean values. Whiskers extend up to 1.5 times the interquartile range. Outliers beyond that distance shown by open circles. Asterisks indicate significance differences (*$p < 0.05$, **$p < 0.01$)

Which species are driving changes?

Indicator species analysis

Species	Group	indval	*p*	Frequency
Vaccinium myrtillus	2006	0.54	0.013	66
Picea abies	2016	0.41	0.021	52
Rubus idaeus	2016	0.31	0.031	22
Epilobium angustifolium	2016	0.30	0.008	13
Epliobium spp.	2016	0.17	0.029	4
Dryopteris carthustiana	Not refuge	0.41	0.049	31
Betula pubescens	Not refuge	0.38	0.032	28
Oxalis acetosella	Not refuge	0.33	0.018	17
Betula pendula	Not refuge	0.29	0.011	15
Epilobium angustifolium	Not refuge	0.26	0.03	13
Maianthemum bifolium	Refuge	0.41	0.005	20

TABLE 2 Significant ground layer indicator species for different years and refuge status

Also, mean Ellenberg value N higher in non-refuges than in refuges

Small trees – the coming canopy?

TABLE 5 Mean number of trees <5 cm diameter counted per plot, standard deviations in brackets

	2006	2011	2016
Picea abies	19.4 (12.64)	14.0 (10.29)	15.4 (11.71)
Fagus Sylvatica	0.15 (0.38)	0.54 (1.13)	1.46 (2.85)
Betula pendula	0.38 (0.96)	0.08 (0.28)	2.08 (4.79)
Betula pubescens	1.38 (2.29)	0.08 (0.28)	2 (3.39)
Sorbus aucuparia	0.62 (1.33)	1.08 (2.63)	1.77 (4.19)
All deciduous	4.15 (3.89)	4.85 (5.91)	9.46 (15.66)

Note. Some species with very low abundances omitted.

- Increase in deciduous species
- However spruce remains by far the most common tree species
- Recolonisation from undisturbed areas?

Conclusions

- Refuge areas have largely unchanged vegetation community.
- In disturbed areas the community has changed- species that can take advantage of increased light and nutrients move in, increase in taxonomic/functional diversity, increase in deciduous tree species…
- However, spruce is regenerating strongly everywhere, recolonising disturbed areas from the unaffected zones- resilient forest?