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Evidenced-based impacts of severe weather events on forestry pests in Scotland: a meta-analysis

Project Final Report



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Forest Research

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Executive Summary

Background and Objectives

This review assesses how forest insect pest species respond to severe weather events (defined here as wildfires, drought, windthrow, and flooding) to better understand how these species or their analogues will respond in Scotland and provide proactive recommendations for management of these species in the future. Climate change is acknowledged as a significant driver of change resulting in changes to the way we manage our forest ecosystems and the way forest invertebrates respond to their environment. The work focused on bark beetles (including *Ips* and *Dendroctonus* species), defoliating moths (including processionary moths and spruce budworms), jewel beetles (*Agrilus* spp.) and sap-sucking insects such as adelgids and aphids that are either present in Scotland or considered potential future threats. To understand how these species will respond and how best to manage these changes we conducted a systematic review of the literature and a meta-analysis of the available evidence.

Key Research Questions

This review and meta-analysis had the following objectives:

1. Systematically review the current literature around forest pest species responding to severe weather events.

2. Conduct a meta-analysis of the published evidence to elucidate how species biology and ecology might change in response to severe weather events.

3. Establish broadly applicable case studies to visualise how future management might occur.

4. Provide evidence-based reasonable management recommendations for land managers and policy makers.

Research

A systematic literature review and meta-analysis was conducted in accordance with PRISMA (Preferred Reporting Items for Systemic reviews and Meta-Analyses) guidelines. Pre-defined search terms were developed by using a combination of systematic software and subject area expertise. To identify studies concerning forest pest responses to severe weather events, the search strategy targeted two key concept areas: key forest pests and invertebrates' biology and ecology, and their responses to the disturbances of severe weather events. Search terms were queried against the online literature database, Scopus, to identify the available relevant literature. The meta-analysis took a standardised mean difference (Hedges *g*) approach with the results validated using robustness analysis such as moderator analysis to explore variance, and funnel plots and leave-one-out analysis to explore publication bias.

As initial search identified 1319 articles of these articles, 1149 were removed during the title and abstract screening stage, 134 were removed during whole article screening, 36 were accepted for use for case studies, and only 8 were deemed to have suitable data for the meta-analysis. However, from these 8 articles, 22 individual "studies" were extracted for use in the analysis.

Main Findings

This study demonstrates that severe weather events can exert contrasting effects on forest pest populations, reinforcing the idea that extreme climatic disturbances alter insect–environment interactions in complex ways. Across the wildfire, drought, and windthrow models, responses varied in both direction and magnitude, highlighting the species-specific and context-dependent nature of pest dynamics post severe weather event.

Wildfire effects on bark borers were generally negative, with the model indicating a small, non-significant decrease in abundance following fire events. Low heterogeneity between studies suggested that differences were likely due to study sampling error. Sensitivity analyses suggested that there was no evidence of publication bias against negative results, although positive publications may be underrepresented, potentially leading to an underestimation of the overall effect size. The wider literature review highlighted that some research has documented post-fire increases in certain bark beetle species (including several North American *Ips* species), reflecting conflicting evidence. These discrepancies are likely species-driven. Some bark beetles, particularly those that evolved under historical fire regimes, appear well adapted to post-fire environments and may exploit newly available weakened or dead host trees. Others may be more vulnerable to direct mortality or habitat alteration caused by fire. This variation suggests that future forest management strategies, especially in regions of Scotland where wildfire risk is increasing due to climate change, must account for the ecological traits of individual pest species. Identifying species already present—or likely to establish—that are adapted to fire-prone systems should be a priority for preparedness planning.

Drought showed a significant positive effect on defoliator larvae performance. Although described statistically as a negative effect on activity, the model demonstrated increased feeding and growth rates under drought conditions, implying enhanced survival and fitness. These findings align with the plant stress and pulsed plant stress hypotheses, which propose that moderate drought can increase foliar nutrient concentration, thereby improving food quality for herbivorous insects. Additionally, drought periods often coincide with elevated temperatures, which can further stimulate invertebrate biological activity, development, and physical activity. Sensitivity analyses suggested that negative drought effects may be underrepresented in the literature, potentially meaning that the beneficial impacts on defoliators are even stronger than currently estimated. However, the small sample size limits confidence in this conclusion. From a management perspective, increasing drought frequency and rising temperatures may elevate defoliator pressure, necessitating improved monitoring and potentially greater reliance on effective pest control measures during drought years.

Windthrow produced a small to medium, non-significant effect on bark beetle abundance, consistent with the prevailing understanding that storm-damaged trees provide breeding material for bark beetles. Nevertheless, some datasets indicated reduced abundance after storms, again suggesting species-specific responses. High heterogeneity among studies indicates that variation was not simply due to sampling error present within each study. Yet, differences could not be explained by pest species, location, or study characteristics within the available data. Other potentially influential variables, such as host tree species or time elapsed since disturbance, were not consistently reported and therefore could not be included. This

underscores the need for more standardized data collection and reporting.

Overall, while these meta-analyses provide a valuable synthesis of current knowledge, they are constrained by small sample sizes, potential publication bias, and inconsistent reporting of key ecological variables. Short-term responses to severe weather are relatively well accounted for, but long-term population dynamics remain poorly understood. Given projected increases in severe weather events under climate change, expanding research on species-specific and long-term pest responses should be a priority, particularly for species likely to affect Scottish forest systems in the coming decades.

Recommendations

This review concludes that the response of forest pests to severe weather events is complex with limited evidence to ground management decisions in. However, there are some logical conclusions from this synthesis that may help land managers and policymakers adapt to the incoming changes due to climate change.

Wildfires are not currently a common threat in Scotland. However, they are predicted to increase in frequency over the next decade and beyond. Therefore, preparedness should be paramount. Whilst the meta-analysis showed varying effects of wildfire on the abundance of bark beetles, the literature highlights potential differences in the way species respond based on their coevolution with fire. Understanding which species are present in Scotland that have evolved with fire may decipher which species need rapid intervention. Therefore, to increase preparedness, we propose to review the key pest species present in Scotland that evolved alongside fire regimes and use distribution data to highlight areas that are most vulnerable to fire aiding those populations.

In this work drought has been shown to be beneficial for leaf defoliating species, with links between periods of drought and outbreaks consistent throughout the literature. Defoliators may need to be prioritised, or vigilance should be heightened, during periods of drought, particularly for events lasting a short period of time. Management responses for leaf defoliators during periods of drought do not appear to differ than typical control. Larval control via pesticides and biocontrol, and adult control via pheromone disruption and trapping were prominent in the literature. However, emphasis must be placed on timely intervention and increased effort. For example, increasing the number of monitoring locations or regularity with which established locations are checked to ensure prompt detection and eradication in sensitive areas.

With the direct evidence for windthrow limited and validation of the model unclear, it is difficult to give evidenced-based recommendations for this severe weather event. Removal of windthrown trees repeatedly appears as a method for reducing available breeding material for bark beetles and thus should be prioritised as a management strategy. Strategically, the priority should be to remove wind-damaged material in high-risk areas, such as forests near ports. Areas where beetle activity is likely to be highest, such as stand edges or storm gaps, uprooted or wind-broken trees, should also be prioritised. This is particularly important to reduce the risk for establishment of *Ips typographus*. The current potential for *I. typographus* establishment in Scotland is moderate, although the current outbreak risk remains low.

However future severe weather conditions mean the beetle could increasingly exhibit primary pest behaviour and pose a substantially greater threat to spruce forests. Higher temperatures can directly impact development rates and phenology (earlier spring flight, increased voltinism) while drought and storm events can provide a surplus of suitable breeding material. This combination could allow this species to cause substantial economic damage if it was to establish in Great Britain in the future. Principal UK forestry species at risk are Norway spruce, as the primary host, and Sitka spruce which is considered a suitable host (Inward *et al.*, 2025).

There are general management recommendations which have commonalities as strategies across the three severe weather events. Firstly, effective monitoring of forest pest species is the first line of defence in management. Evidence consistently shows that prompt discovery of new invasions or outbreaks, particularly for bark beetles and leaf defoliators, results in better management outcomes, therefore monitoring should continue to be supported. Secondly, supporting sanitation felling and thinning of vulnerable hosts is critical for reducing the likelihood of pests establishing or thriving post severe weather event. These proven strategies should be targeted at high-risk areas. Finally, in the long-term Scotland should be seeking to develop more resilient forest ecosystems. Same-age, single-species stands are commonplace in some productive forestry systems and increasing both species and age diversity can improve resilience to natural disturbances and tree pests and diseases. Providing more resilient and diverse forest ecosystems will not only create forests more resilient to pest establishment, but will also facilitate ecosystem functions such as biocontrol to help to suppress populations of difficult to manage pests such as sap-sucking insects.

Ultimately, how we manage forest pests in the future will require varied management techniques and proactive decision making. Whilst this review and meta-analysis have been able to show how some forest pests species respond to severe weather events and provide some management recommendations, we also highlight how limited our understanding of these species biology and ecology is. These critical gaps in our knowledge could be addressed by enhancing our fundamental understanding of forest invertebrate ecology and life history. This information would increase our ability to develop more precise management responses to a wider range of forest pests, thus securing forest health across Scotland in the face of challenges to come.

1 Introduction

Anthropogenic climate change is a prominent challenge expected to impact the way in which countries manage their natural resources and ecosystems over the 21st century (Mantyka-pringle *et al.*, 2012). One of the main threats posed by climate change is the exacerbation of severe weather events. In Scotland, this is predicted to include more frequent and intense storms, flooding in high-risk areas, longer periods of drought and increasing risk of wildfires. Severe weather events can disrupt environmental conditions, which can then act as catalysts for change in the way that many species interact with their environment, including species that are considered pests for forests and woodlands (**Error! Reference source not found.**). These environmental changes can play a large role in forest pest biology and ecology with both positive and negative outcomes for these species. For example, increased storms can provide additional susceptible hosts e.g. windblown trees for bark beetles leading to increased opportunities for breeding and enhanced distribution. Windthrow from storms has been directly linked to *Ips typographus* outbreaks across Central Europe (Marini *et al.*, 2017). Alternatively, severe weather events can negatively affect invertebrate populations by creating unfavourable conditions e.g. wildfires destroying habitat (Holmquist *et al.*, 2024, Wermelinger *et al.*, 2025). Additionally, the development rates and dispersal of most insects are directly linked to temperature. Species that are adapted to a narrow temperature range react to higher temperatures by shifting northwards, in contrast to those able to withstand broader temperature fluctuations which demonstrate less movement. Other groups are influenced more by moisture availability than by temperature (Hällfors *et al.*, 2024).

Understanding how pest species respond to these severe weather events is essential, particularly as climate change drives an increase in their frequency and severity. Many pest species are adapted to survive these extremes and may thrive as these events become more common. However, our current understanding of the way in which these species respond to severe weather events is insufficient to tackle the challenges ahead. By collating the available literature on current priority pest species or families and how they may succeed or fail after severe weather events in their environment, it will be possible to provide preliminary recommendations on which species are most important to prioritise for management in the future climate. It will also highlight where knowledge gaps are present, showcasing which species and scenarios decision makers may need to prioritise for research.

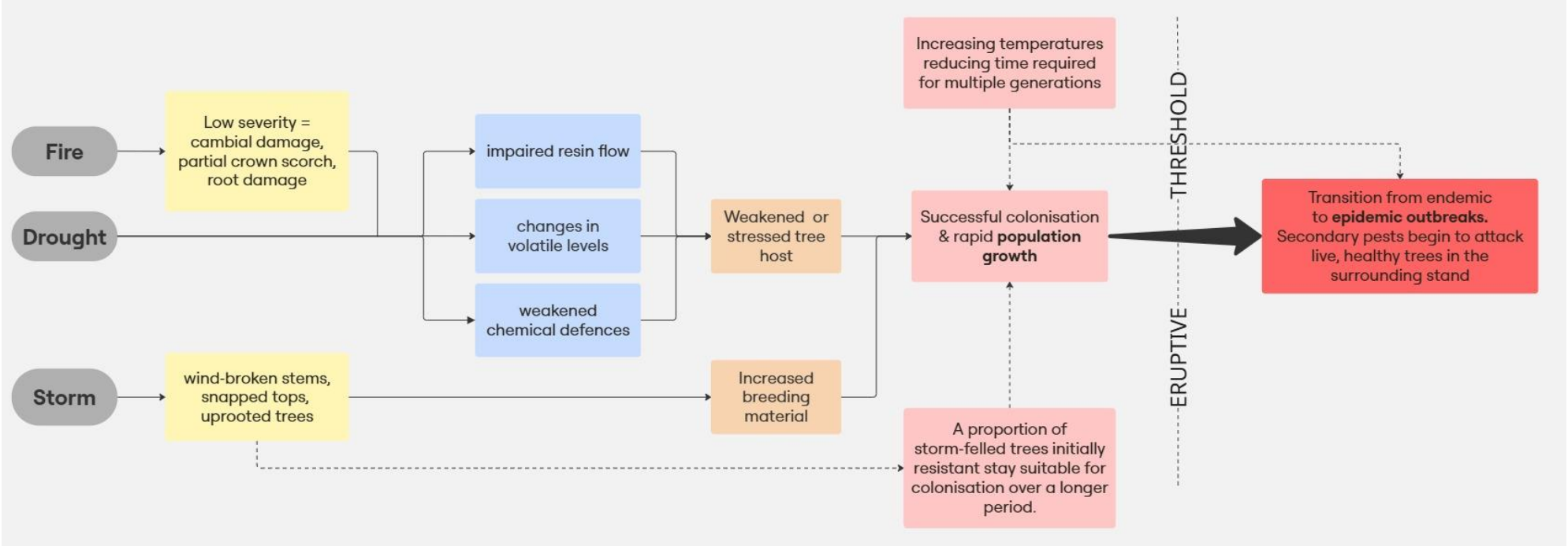

Figure 1: Severe weather events (drought, storms, fire) either weaken tree defences or create abundant material that secondary bark beetles can readily colonise; successful reproduction in this material increases beetle populations until a threshold is reached at which mass-attacking beetles can overcome the defences of nearby healthy trees, leading to epidemic outbreaks.

2 Materials and Methods

2.1 Data collection

A systematic review and meta-analysis were conducted in accordance with PRISMA guidelines (Page *et al.* 2021), this involved using pre-defined search terms developed in the R package *Litsearchr* which were queried against the Web of Science literature database to evaluate evidence for the ecological and biological responses of forestry invertebrate species to severe weather events (Page *et al.*, 2020) (defined here as wildfire, windthrow, flooding, or drought).

2.1.1 *Systematic review*

Litsearchr utilises two main steps to help build search terms. It identified which papers are often cited together to establish the relationships between them and scans the text of known relevant papers selecting keywords that appear frequently. A small set of key search terms is used to run a simple test search, and the results are then used to create a list of all the keywords from those papers to use in the literature search. This list was then curated with the team's expertise to form an optimal search string.

To be included in the database, studies had to meet all the following criteria:

- Mention a pest species of concern for Scottish forests and woodlands and identified as a priority by the project team utilising guidance from the UK Plant Health Risk Register (UKPHRR).
- Report a change in a biological/ecological factor (such as abundance, feeding rate, etc.) (hereby referred to as responses) in paired sites prior to and post severe weather event.
- Attribute any changes to the target species directly to, or very likely to be caused by, the impacts of the defined severe weather events.
- Report data with mean, sample size, and variance (standard deviation (SD), standard error (SE), or confidence intervals).
- Be published in either English or German, reflecting the language capabilities of the project team.

For all eligible studies, data were extracted on species identity, geographic location, forest or habitat context, severe weather type, response variables measured and main outcomes. Evidence was then collated from these sources, prioritising those studies which are relevant to GB, and then evaluated. Response variables measured that were sought from each study were; abundance, distribution, dispersal capability, fecundity, voltinism, feeding/attack rate, growth rate. Data were extracted for each species response to a severe weather event from each article using a predefined data extraction spreadsheet. Each species response is hereby referred to as a separate 'study' and is considered an individual data point.

2.2 *Meta-analysis*

The statistical analysis used established meta-analysis methods implemented in the R package "metafor" to check for bias (Viechtbauer, 2010), to calculate effect sizes and run the model, in R version 4.4.2. The meta-analysis broadly followed the guidance of Koricheva *et al.* (2013) and Koricheva & Gurevitch (2014), which although originally written for plant ecology is still applicable. This included providing a database of all studies included in the analysis, testing whether the results are sensitive to potential biases in the underlying studies by using a trim-and-fill analysis to test for asymmetry in effect sizes, and using a "leave-one-out" approach to see how much each individual study influenced or skewed the results.

The strength and direction of responses to severe weather events was assessed using Hedges' g, which is an effect size that works well when sample sizes differ and can correct for small sample sizes (Hedges & Olkin, 1985; Koricheva *et al*, 2013). For each study, Hedges' g was calculated from the reported mean abundance of the species and the associated variation (standard deviation) at paired sites before and after a severe weather event. Where only standard error was reported, this was converted to standard deviation so that all studies were treated consistently.

Two types of statistical models were fitted: a random-effects model and a mixed-effects model. The random-effects model was used as the main approach as it allowed for real differences among studies (for example, different locations, species or methods). Secondly the mixed-effects model (or moderator analysis) was generated to explore how responses vary with factors such as species or type of severe weather event, examining why species-specific responses vary in magnitude with different types of severe weather events (Koricheva *et al*, 2013). On this basis, implications for forest and land management strategies in Scotland were identified, with particular emphasis on whether reported changes in dispersal, fecundity, voltinism or survival under severe weather conditions are expected to alter pest risk.

3 Results

3.1 *Data Collection*

The following search string which was based on the *Litsearchr* output and expert opinion was queried in September 2025, (("forest* insect*" OR "forest* pest" OR "insect") AND ("severe weather" OR "extrem* weather*" OR fire* OR "forest* fire*" OR drought OR "drought* condit*" OR wind* OR storm* OR flood*) AND (population* OR "population change" OR "reproduct* success" OR abund* OR distribution OR biology OR lifecyle OR fecundity) AND (impact* OR stress*) AND NOT (horticulture OR crop OR agriculture OR marine OR aquatic OR benthic OR freshwater OR greenhouse)).

This generated 1319 articles following which the project team was divided into two independent review teams, to ensure systematic evaluation and reduce selection bias, with both teams holding expertise in forest invertebrate ecology and biology, and UK plant health risks. Of the initial 1319 articles, 1149 were removed during the title and abstract screening stage, 134 were removed during whole article screening, 36 were accepted for use for case studies and had metadata extracted, and only 8 were deemed to have suitable data for the meta-analysis (

Figure 2).

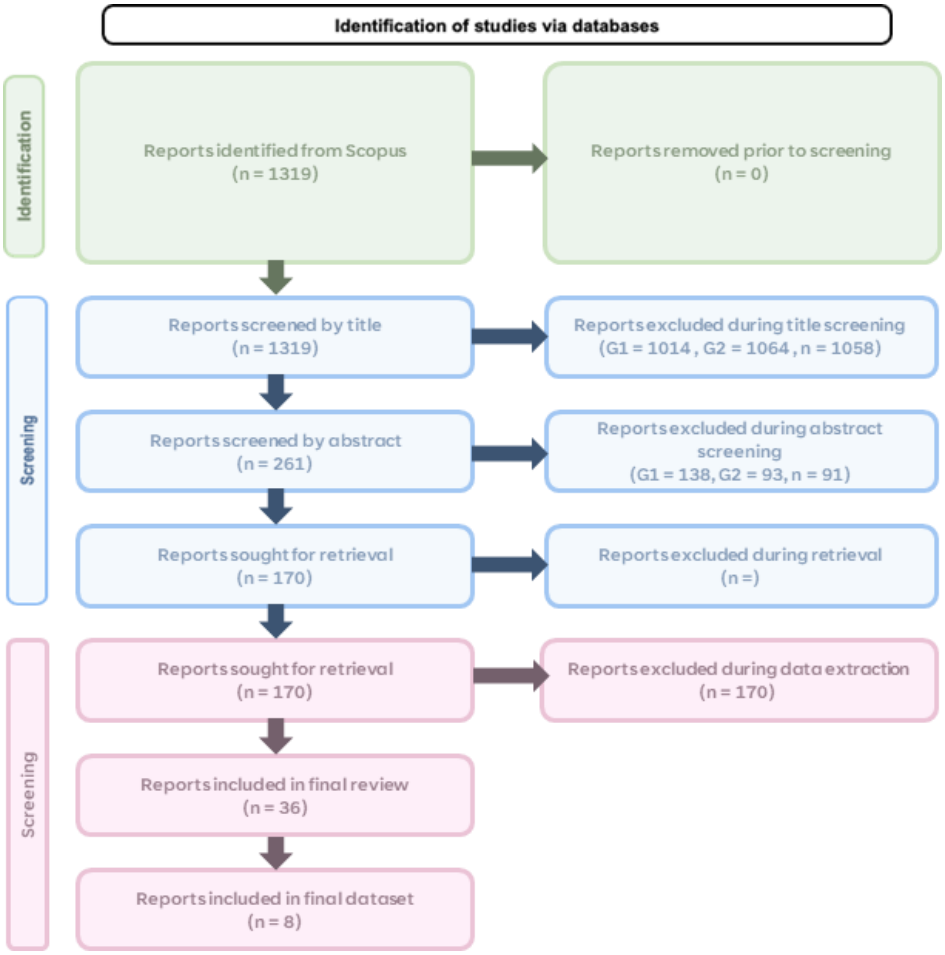

Figure 2: PRISMA workflow of the systematic review indicating the number of articles included and excluded at each stage of the review. Each article and any subsequent data extraction was subject to independent review across the two teams which occurred at each stage, with consensus being required before proceeding to following stages.

3.2 Meta-analysis

Of the 8 journal articles that were included in the final dataset 22 "studies" from 3 countries were able to be included across the three severe weather event models (Figure 3). The studies included in the meta-analysis covered a range of forest pest species representing functional groups, including bark beetles (*Ips* spp., *Dendroctonus* spp.), defoliating moths, and jewel beetles (*Agrilus* spp.). The complete list of species examined is presented in Appendix 2, Table 1. Due to the limited number of studies (n=22), analyses were conducted at the feeding-guild level rather than for individual species. The resulting models therefore indicate general trends for bark borers (n=18) and defoliators (n=4) recognising that responses may vary among individual species within each guild. (Figure 4). It should also be noted that the models presented here are reflective of data availability. For instance, while we were able to generate models testing the effects of wildfire on bark beetles this was not so for defoliators due to a lack of studies testing these effects.

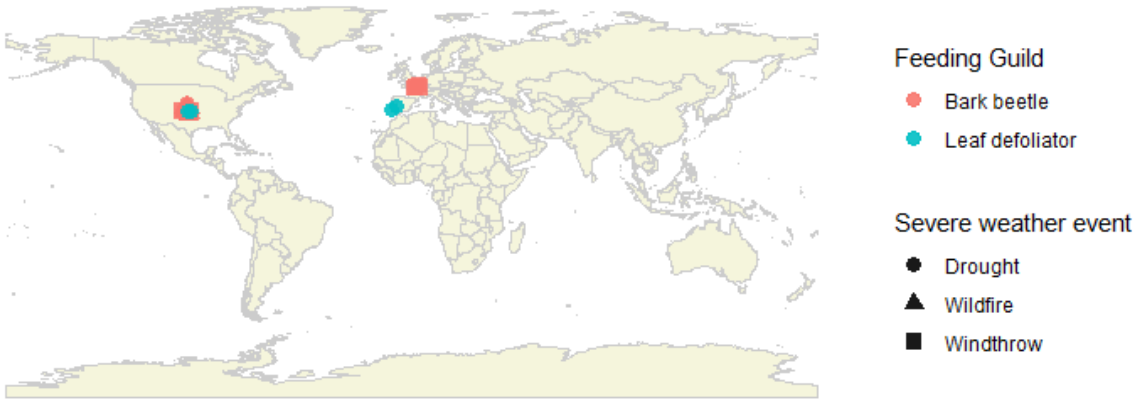

Figure 3: Map of study locations for the 22 studies included in the meta-analysis, with points filled based on the focal feeding guild of the study and outlined based on the severe weather event.

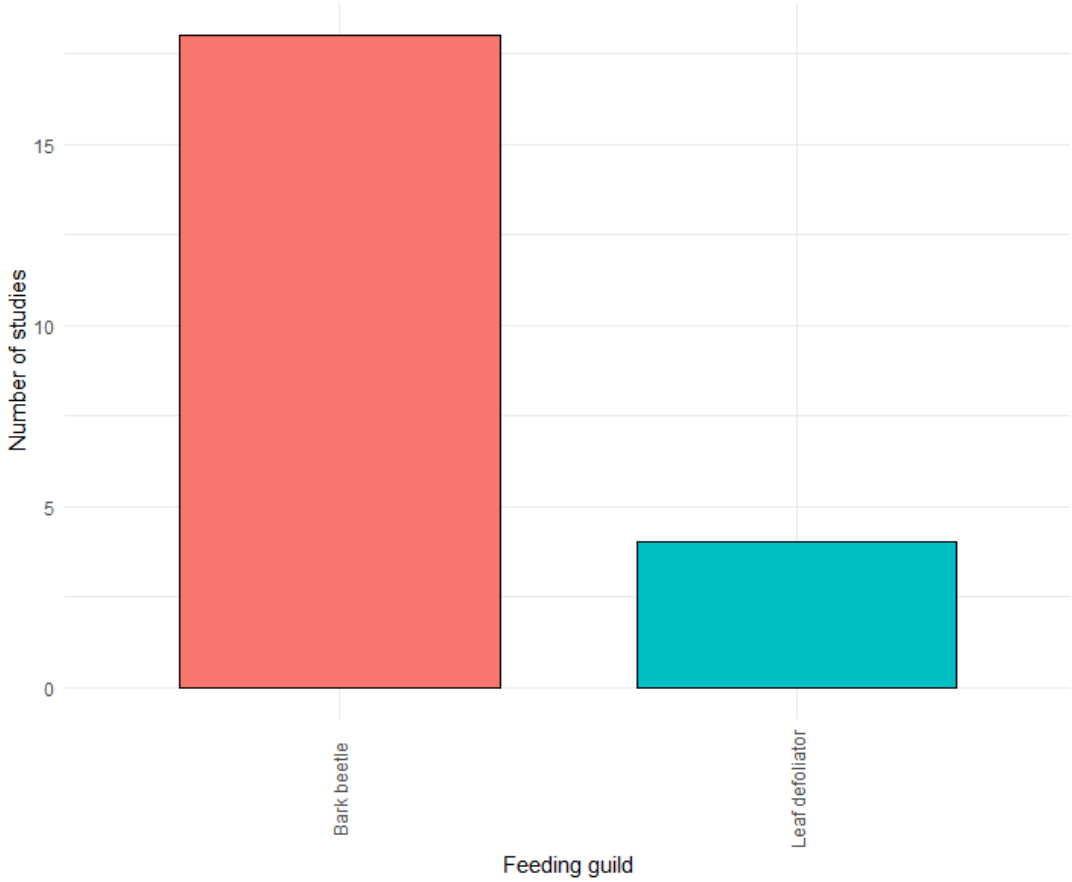

Figure 4: The number of studies that included the two feeding guilds. The full species list can be found in Appendix 2.

3.2.1 Wildfire

Wildfire was associated with a small positive effect on the abundance of bark borers (Hedges' g = 0.26, 95% CI: −0.04 to 0.55), with this positive effect indicating a reduction in the abundance of bark beetles. This effect was not significant (z = 1.70, p = 0.09) confirmed via the permutation test (p = 0.25). Finally, there was no between-study heterogeneity detected for this analysis as shown via the Cochran's Q test (Q_9 = 5.80, p = 0.76), suggesting effect size variance was primarily explained by sampling error in these studies alone. It should be noted however that whilst this model had the largest sample size of the three (k = 10) this is still

considered a low sample size. The moderator analysis for this model showed that moderators, such as location and species, were able to explain the between-study heterogeneity and the observed differences between studies were due to an unknown factor.

Visual inspection of the funnel plot shows no distinct asymmetry suggesting limited to no publication bias was detected. Although, trim-and-fill analysis suggested there were missing studies on the right side of the plot highlighting an underrepresentation of positive effects.

3.2.2 Drought

Drought was associated with a large negative effect on the activity of defoliator larvae (Hedges' g = -2.4, 95% CI: -3 to -1.5), with this negative effect indicating an increase in the feeding and growth rates of defoliator larvae. This effect was considered significant (z = -5.82, p = <0.001) by the model however this was overruled by the permutation test (p = 0.125) suggesting that the effect is not statistically robust. There was no between-study heterogeneity for this analysis as shown via the Cochran's Q test (Q_3 = 2.93, p = 0.40) however, this model had the lowest sample size (k = 4) limiting the robustness of this test. The moderator analysis for this model showed none of the moderators were able to explain the between-study heterogeneity.

Visual inspection of the funnel plot shows slight asymmetry to the right side of the plot. Additionally, trim-and-fill analysis reflects this suggesting that there are potential studies missing from the left side of the plot highlighting an underrepresentation of negative effects. Leave-one-out analysis shows that no one study was driving the overall result.

3.2.3 Windthrow

Windthrow was associated with a small to medium negative effect on the abundance of bark borers (Hedges' g = -0.38, 95% CI: -1.5 to 0.69), with this negative effect indicating an increase in the abundance of bark borers. This effect was considered not significant (z = -0.7, p = 0.3) by the model which was confirmed by the permutation test (p = 0.35). There was high between-study heterogeneity for this analysis as shown via the Cochran's Q test (Q_7 = 23.96, p = <0.05) (k = 8). The moderator analysis for this model showed none of the moderators were able to explain the between-study heterogeneity.

Visual inspection of the funnel plot shows horizontal stretching with extreme effect sizes on both sides which suggests high heterogeneity (validated by the Cochrans' Q test). Trim-and-fill analysis did not suggest that there were missing studies from either side of the plot and leave-one-out analysis did not suggest that any one study drove these results.

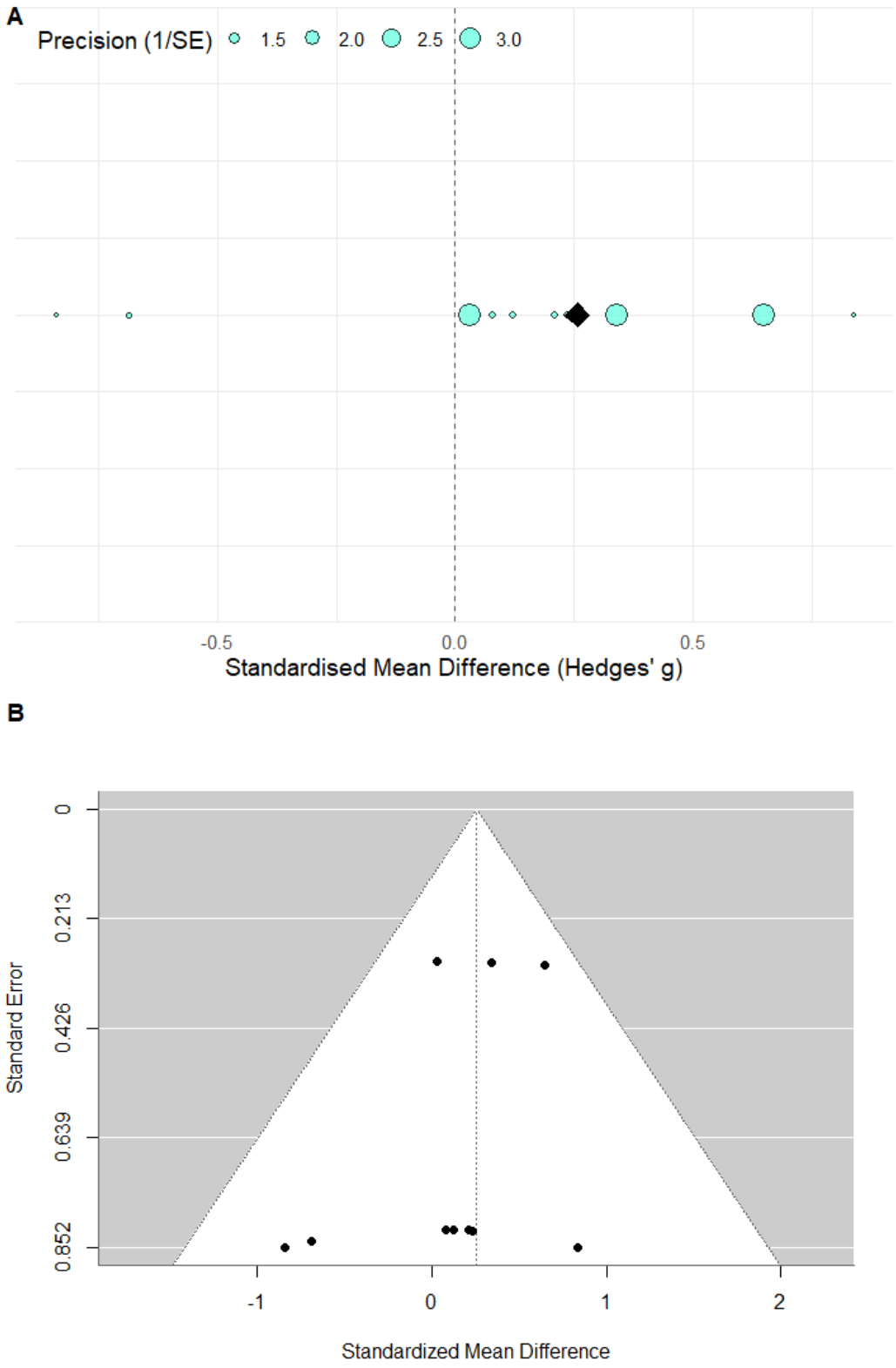

Figure 5: The upper plot shows abundance responses of bark beetle species to wildfires with the black diamond showing the overall standardised mean difference for the studies considered. The translucent circles represent individual species responses extracted from each article. The size of each circle is proportional to its relative weighting in the overall model. A positive effect size means that wildfires reduce abundance in bark beetles. The lower plot shows a funnel plot of the meta-analysis showing a normal spread of studies indicating little publication bias and low heterogeneity.

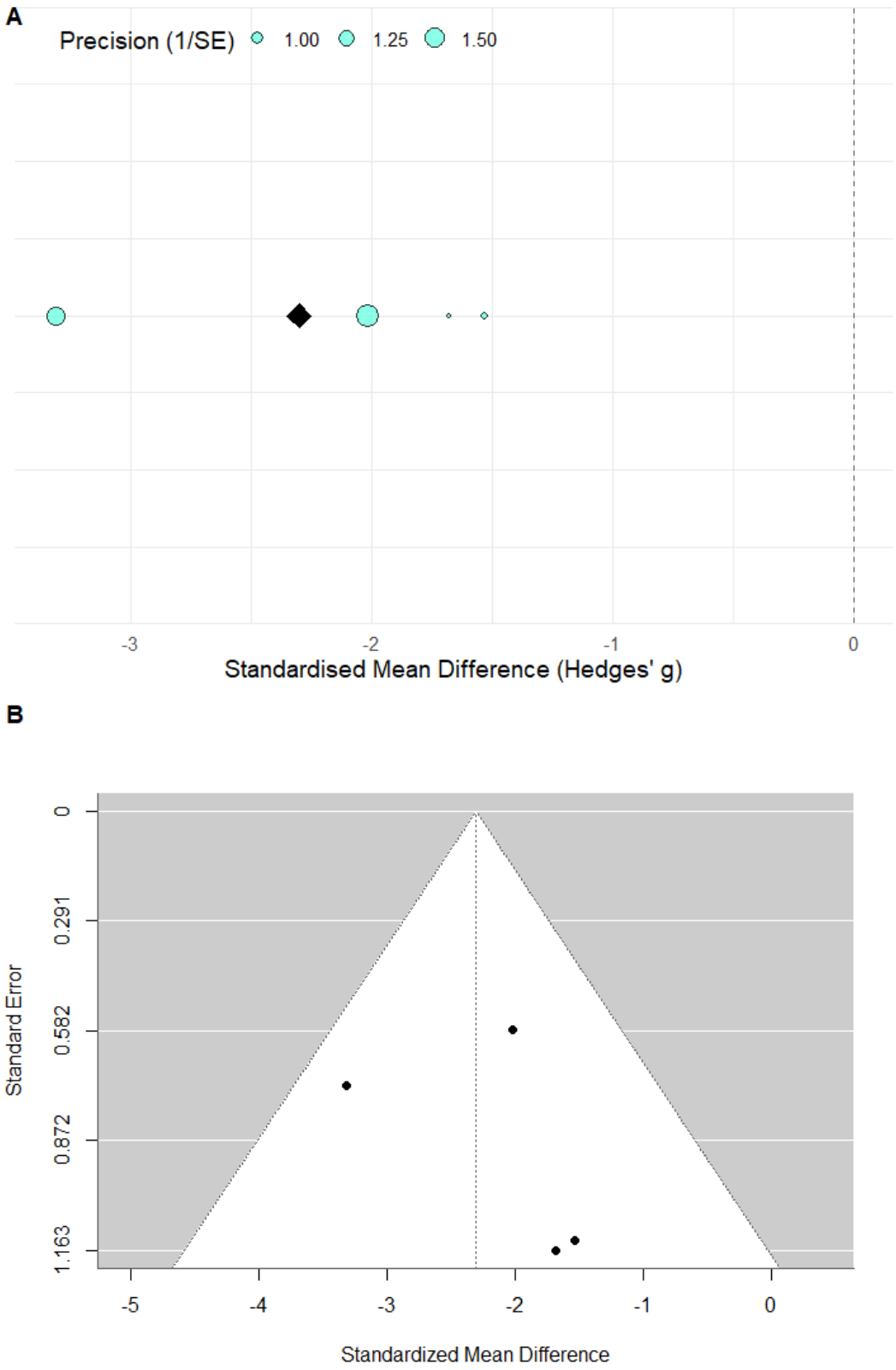

Figure 6: The upper plot shows activity responses of leaf defoliator species to droughts with the black diamond showing the overall standardised mean difference for the studies considered. The translucent circles represent individual species responses extracted from each article. The size of each circle is proportional to its relative weighting in the overall model. A negative effect size means that droughts increased the activity of leaf defoliators. The lower plot shows a funnel plot of the meta-analysis showing a slight bias of studies with positive effects and little heterogeneity.

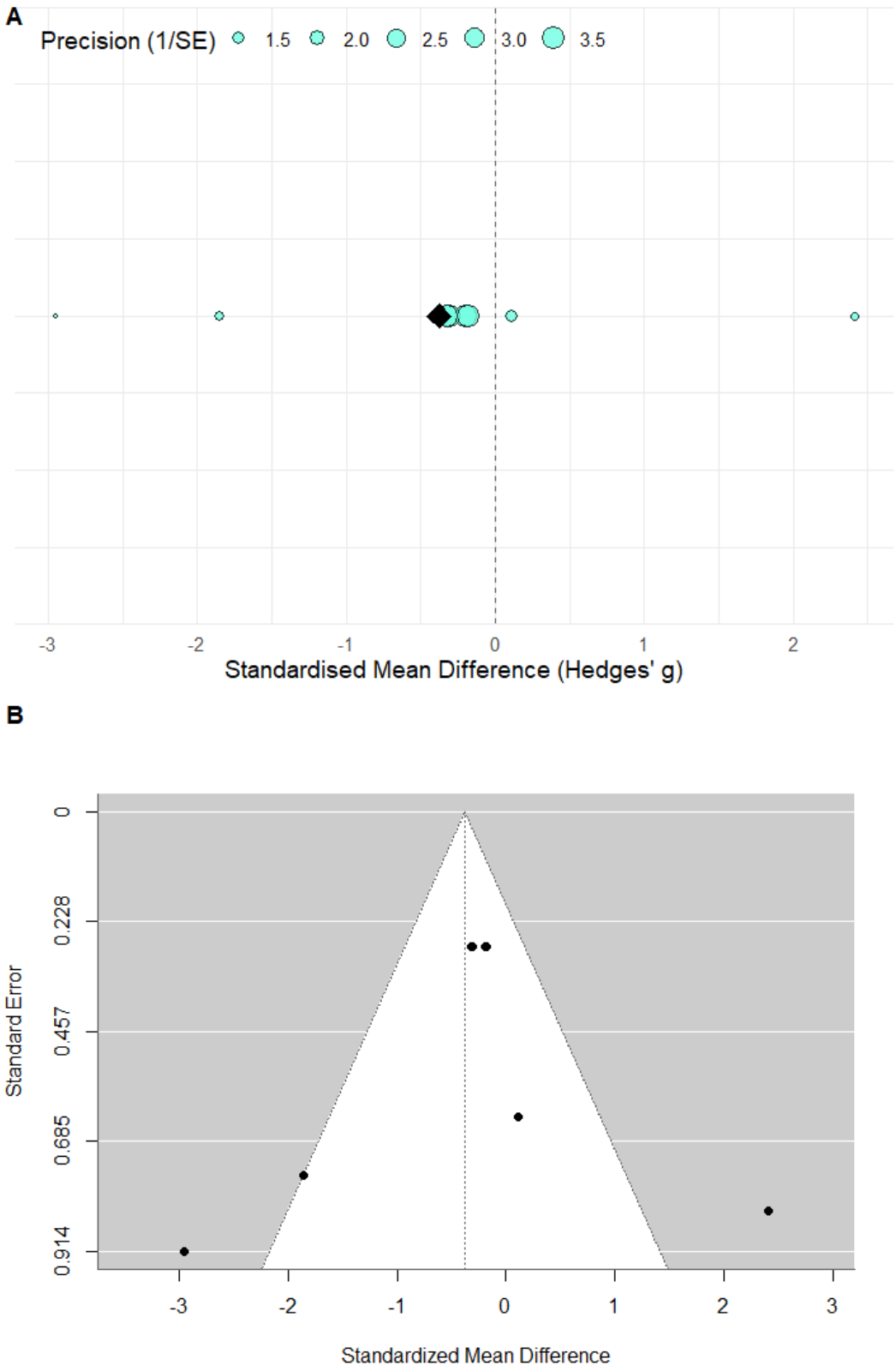

Figure 7: The upper plot shows abundance responses of bark beetle species to windthrow with the black diamond showing the overall standardised mean difference for the studies considered. The translucent circles represent individual species responses extracted from each article. The size of each circle is proportional to its relative weighting in the overall model. A negative effect size means that windthrow increases the abundance of bark beetles. The lower plot shows a funnel plot of the meta-analysis indicating little publication bias and high heterogeneity.

4 Discussion and Recommendations

Our results show that severe weather events can have mixed effects on population dynamics of forest pests. This study therefore corroborates the assumption that severe weather events can change how insects interact with their environment. All three models displayed different trends, each with varying degrees of severity, highlighting the complexity of species responses to extreme weather events.

4.1.1 Wildfire

Wildfires can shape ecosystems and influence biodiversity (Jaworski, *et al.* 2025). Whilst not yet common in Scotland, the threat of wildfires is increasing due to climate change and understanding what role they will play in Scottish forests is therefore paramount. The respective model shows that wildfires typically decrease bark borer abundance, however this effect is small and non-significant. It should be noted that the sensitivity analysis also indicated that any positive effects observed (i.e. decrease in abundance) was based on a limited data set and in future incorporating further data may alter both the magnitude of the effect size and its statistical significance. Additionally, some studies showed increasing bark borer abundance post-wildfire (Campbell, *et al.*, 2008). These results reflect the conflicting evidence in the literature surrounding bark beetle abundance post-wildfire and are likely driven by the species of bark beetles present in these studies. Several bark beetles, such as *Dendroctonus terebans*, have evolved alongside fire regimes and are either more robust to the effects of wildfires or able to take advantage of a post-wildfire landscape in a way that other bark borers cannot (Campbell, *et al.*, 2008, Lindenmayer, *et al.*, 2025). This discrepancy shows that future management decisions will depend on the bark beetle species. To aid preparedness for the increasing risk of wildfires, we suggest identifying forest pest species that evolved alongside wildfires and focusing on those already present in Great Britain and/or Scotland or those likely to be establish over the next decades.

4.1.2 Drought

The results of the drought model show that drought has a significant negative effect on the activity of defoliator larvae. For this group the model demonstrates increased feeding and growth rates under drought conditions, suggesting better survival outcomes. This is in line with two hypotheses: the plant stress hypothesis and the pulsed plant stress hypothesis. These suggest that periods of drought concentrate beneficial nutrients in plant foliage, leading to better fitness outcomes for defoliator larvae (Bauerfeind and Fischer, 2013; Moise *et al.*, 2019). Additionally, periods of drought likely coincide with periods of increased temperatures, which are linked to increased activity and growth rates in many invertebrates (Nedvěd, 2009). Therefore, temperature is an additional factor to consider during drought years, which may aid defoliators. As droughts are expected to become more common and average temperatures are expected to increase under future climate change scenarios, it is vital to understand how both factors interact and influence defoliators (Kirkpatrick Baird, *et al.* 2023).

The sensitivity analysis for this model is noteworthy as it suggests an underrepresentation of negative effects from the available studies, suggesting that drought may be even more beneficial to defoliator larvae than detailed within this study. The results further corroborate the alleged beneficial fitness outcomes suggested in the plant stress hypothesis and pulsed

plant stress hypothesis and should be considered in future management decisions. However, due to the small sample size for this model the sensitivity analysis may not be robust, so results should be interpreted cautiously.

The anticipated positive impact on defoliators under drought conditions has two important management implications. Firstly, maintaining access to effective pesticides will be critical for reducing damage by limiting larval populations. Secondly, if drought conditions improve defoliator fitness and survival, enhanced monitoring and trapping programmes may be warranted to detect and capture increased numbers of adults, thereby reducing reproductive output and limiting population growth in subsequent years.

4.1.3 Storm

Windthrow is a prominent focus for forest managers and a key component in affecting forest pest populations (Havašová, *et al.*, 2017). The windthrow model shows a non-significant, small to medium negative effect on bark beetles which indicates a positive impact on bark beetle abundance. This is in line with contemporary thinking surrounding windthrow effects. However, some of the included datasets indicate decreases of bark beetle abundance post-storm event. Similar to the results of the wildfire model, there is potentially a species-specific effect occurring. The high heterogeneity between studies supports this assumption and further suggests that the difference in effect sizes was not driven solely by sampling error. The analysis indicated that the observed differences could not be accounted for by looking at individual forest pest species. Additionally, other factors such as location and study did not explain this high heterogeneity. Factors not included in this analysis, like tree species or time since weather event, may be better at explaining the variation, but this study lacked sufficient data to incorporate these variables into the moderator analysis. Including a larger number of pest species may also have reduced high variability in the results. This highlights the importance of consistent data reporting and the need for more studies which investigate these effects.

4.1.4 General

Some caveats should be considered when interpreting the results of the presented meta-analyses. Firstly, the small sample sizes for all three models are likely to reduce reliability of the results, although statistical measures were used to account for this. For instance, the sensitivity analysis indicated that there is data missing from multiple models. This is typically the result of publication bias limiting the availability of studies with negative results and thus tempering potential effects. The models provide a useful overview of the current evidence have, but also highlight how little data exist to clearly show how severe weather affects forest pests. We suggest further research in this area should be a priority to better understand individual species responses to severe weather events, particularly those that are predicted to have large impacts on Scottish forestry in the future.

A further limitation is the inconsistent reporting of variables across the literature, which prevented their inclusion in the models. One such variable is the time elapsed since the severe weather event. Many studies reported immediate responses to severe weather events and whilst this data is useful, we are unable to elucidate long term reactions of pest species. For instance, in the short-term defoliator larvae increase their activity during drought, however, prolonged drought conditions may severely reduce food availability or increase heat stress

thus compromising long term fitness. Likewise, wildfire can reduce the abundance of bark borers in the short term by killing them. However, long term, wildfire may provide more available hosts and lead to an increase in abundance.

4.1.5 Case Study 1: Bark beetles

4.1.5.1 Introduction

This case study focuses on bark-boring beetles (Curculionidae: Scolytinae) with emphasis on the two genera *Ips* and *Dendroctonus*. Of particular concern is the eight-toothed spruce bark beetle, *Ips typographus*, a major pest of Norway spruce across continental Europe, currently not established in Great Britain.

All species discussed are phloem-feeding bark beetles with four developmental stages: egg, larva, pupa, and adult. Adults bore through the outer bark to construct breeding galleries within the phloem. After hatching, the larvae feed on the phloem before pupating in chambers at the ends of larval tunnels. The development time for larvae is dependent on the physiology of the individual species and local thermal conditions (Six and Bracewell, 2015). This dependence on thermal conditions for generation time can also be exploited to increase populations when host and weather conditions are suitable (Franceschi *et al.*, 2005; Bentz *et al.*, 2010). Adults are the only dispersal stage and are responsible for host selection and colonisation. The principal host of *I. typographu*s is Norway spruce, an economically important species across Europe. In Scotland, spruce stands form significant components of commercial forestry. Principal UK forestry species at risk are Norway spruce, as the primary host, and Sitka spruce which has recently been confirmed as a suitable host (Inward *et al.*, 2025). Outbreaks in central Europe have caused extensive tree mortality. When beetle populations exceed threshold densities, mass attack strategies allow them to overcome host resin defences and attack and kill healthy trees.

4.1.5.2 Affected traits under severe weather events and impact of bark beetles

Storms and wind damage are consistently attributed as having a strong influence on bark beetle populations, by providing breeding material in the form of windthrown and wind-broken trees. Following major storms across central Europe and Scandinavia, outbreaks of *I. typographus* have frequently occurred with shifts in behaviour as secondary pests to primary pests (Göthlin *et al.*, 2000; Holuša and Fiala, 2025). This has resulted in seemingly healthy trees becoming subject to infestation and in many cases the damage caused by the pest can exceed the initial storm damage.

Drought and elevated temperatures have potential to further influence beetle dynamics through both direct and indirect mechanisms. Bark beetles exhibit temperature-dependent development which is a critical mechanism enabling mass attack and successful host colonization (Creeden, Hicke and Buotte, 2014). Warmer summers may accelerate larval development and permit completion of additional generations and sister broods (Rouault *et al.*, 2006; Gilbert *et al.*, 2005; Wermelinger and Seifert, 1999). Concurrently, drought reduces tree resin flow and impairs defensive capacity, which has been linked to increase colonisation success in species such as *Dendroctonus ponderosae* (Amman, 1972; Amman and Pasek, 1986; Boone *et al.*, 2011). These interacting effects may enable populations to surpass eruptive thresholds. However, prolonged or extreme drought may reduce phloem quality, lowering

brood survival in later outbreak phases (Safranyik and Carroll, 2006). *Dendroctonus micans*, which is present in Scotland, typically causes little mortality across most of its range, but drought has been linked to outbreak initiation at expanding infestation fronts (Grégoire, 1988; Rolland and Lempérière, 2004)

The effects of wildfire or prescribed fires on pine feeding *Ips* are variable. Effects appear to depend on the severity of the fire (McCullough *et al.*, 1998). In some instances, low severity fires can increase resin flow, bolstering tree defences, or they can sufficiently stress hosts to allow for colonisation. High severity wildfires may actively kill beetles, render phloem unsuitable for beetle development, or completely remove hosts from the landscape (McCullough *et al.*, 1998). The responses for most *Dendroctonus* to wildfire appear to be similar with low severity fires supporting endemic populations but larger fires reducing host availability and increasing competition between saproxylic species (Elkin and Reid, 2004; Powell, Townsend and Raffa, 2012). However, two species of *Dendroctonus* (*Dendroctonus pseudotsugae* and *Dendroctonus valens*) show evidence of preferentially targeting trees stressed by drought and wildfires with both severe weather events linked to outbreaks of these species (Cunningham *et al.*, 2005; Hood and Bentz, 2007; Six and Bracewell, 2015; Six and Skov, 2009).

4.1.5.3 Response, monitoring and control

Several high profile species of *Ips* and *Dendroctonus* are not present in Scotland therefore management should aim at prevention and surveillance through existing monitoring networks, with focus on high-risk entry points, including ports and processing facilities. Pheromone-baited traps provide effective early detection tools for *Ips* species and should be deployed strategically in vulnerable regions.

In order to minimise risk of establishment in the case of accidental introduction, rapid removal or processing of wind-damaged timber following storm events, prior to the next flight season, is critical. This can be a considerable task, meaning certain areas may need to be prioritised by factoring information such as; stand composition, stand density, and age-class (Nikolov *et al.* 2014). Additionally, monitoring is likely to play an important role post-windthrow as early detection is vital to successful outcomes. Evidence from outbreaks in Canada shows that the size of the initial infestation strongly influences long-term outcomes, with early direct control significantly reducing the area affected over subsequent years (Carroll *et al.,* 2017). Sanitation felling of severely stressed trees post severe weather event and prioritisation of high-risk stand edges or storm gaps may further limit outbreak risk. Additionally, biological control may play a key role in suppressing outbreaks post severe weather event. Introduction of the specialist predator *Rhizophagus grandis* has proven highly effective in suppressing *D. micans* populations, with 60–80% of brood chambers colonised during outbreaks in Belgium and Georgia respectively, providing strong stabilising pressure on populations (Grégoire, 1988).

Long term responses should focus on developing resilience into Scottish forests and forestry with woodland creation and planting of crops prioritising the promotion of mixed-species stands and structural diversity. This avoids extensive monocultures of highly susceptible hosts, which increases the area available for attack and increases the probability of establishment and facilitates the spread of pests.

4.1.6 Case Study 2: Moth Defoliators (e.g. Budworm/Oak processionary moth)

4.1.6.1 Introduction

Several defoliators are of concern to Scottish forests, this case study highlights two of high-profile groups considered a particular threat, i.e., processionary moths (Notodontidae) and spruce budworms (Tortricidae). The two processionary moth species of concern are oak processionary moth (*Thaumetopoea processionea*, OPM) and pine processionary moth (*Thaumetopoea pityocampa*, PPM). OPM are associated with *Quercus* spp. feeding on both, pedunculate oak (*Quercus robur*) and sessile oak (*Quercus petraea*), native to Scotland (Roques, 2015). PPM is associated with *Pinus, e.g.,* Scots pine (*Pinus sylvestris*) and lodgepole pine (*Pinus contorta*), and other coniferous trees such as European larch (*Larix decidua*) (Roques, 2015). Both species are native to central and southern Europe and some areas of North Africa, but have been steadily expanding northwards over the last decade. OPM was imported to the UK in 2006 and has since established and spread in the South-East of England despite extensive management efforts (Miller, *et al.*, 2026). Four spruce budworm species of concern within this case study are; the western spruce budworm (Choristoneura freemani), eastern spruce budworm (Choristoneura fumiferana), and two species of black-headed spruce budworm (Acleris gloverana and Acleris variana) which feed on a range of spruces, pines, and firs (Flower, *et al.*, 2014; Xu, *et al.* 2019). All are native to North America (USA and Canada) and absent from Great Britian.

All of these defoliators are univoltine but each species development cycles vary. OPM eggs are laid at the terminal ends of branches with hatching coinciding with budburst. Larvae feed over summer, before pupating and emerging as adults in late summer to breed (Battisti, *et al.*, 2006). PPM larvae hatch in late autumn and feed during winter before pupating in early spring. Adults then emerge in midsummer to breed (Rocha, *et al.*, 2020). Both species build communal nests as larvae which are spun from silk and comprise the urticating hairs that are the source of human health issues. The two *Acleris* species follow a life cycle similar to that of OPM with larval emergence coinciding with budburst in the spring followed by pupation in the summer, although development times for these two species can vary dramatically. The *Choristoneura* species hatch prior to winter where larvae overwinter in hibernacula and emerge the following spring as a stage two instar (Moise, *et al.*, 2019). Development continues from there with pupation occurring in summer.

4.1.6.2 Affected traits under severe weather events and impact of defoliators

Direct evidence from the meta-analysis suggests that the mentioned species benefit from drought conditions, with accelerated development and increased feeding rates. Whilst the direct impact to tree hosts has not formally been recorded, long term this may result in higher host mortality than has previously been observed from these moths (Rouault, *et al.*, 2006; Bao, *et al.*, 2019). It has been established in this work that drought conditions coinciding with increased temperature led to increased activity. It is entirely possible that this would also affect adults by providing more frequent, or longer, periods where flight is possible thereby allowing species to travel farther or for more individuals to fly during certain periods - aiding with overall dispersal (Roques, 2015). Furthermore, heavy winds which allow for windthrow will likely be beneficial in helping the dispersal of adults. This has been noted with several male OPM specimens caught in light traps on the southern coast of England, thought to have been aided by strong winds in crossing the English Channel. Wildfires are likely to be heavily

damaging to defoliator populations through several mechanisms: actively killing individuals, the destruction of primary feeding material, and by destroying shelter making them easier to predate.

4.1.6.3 Response monitoring and control

The focus of management measures should be to prevent introduction of any of these species into Scotland. Due to OPM populations being present in England and thus more likely to arrive via land travel, this species should be prioritised. Especially during and following drought events, monitoring via pheromone and light traps should be intensified, above the usual recommended baseline to be vigilante for any increased spread.

The evidence presented for defoliator response during drought can only be attributed to these species. However, during drought years, or for short periods post drought, it may be prudent to prioritise robust application of the following management techniques for other Notodontidae and Tortricidae. Firstly, timely application of larval control where appropriate to counteract any fitness benefits. Secondly, targeted application of pheromone disruption to reduce the spread of adults and success of breeding. Finally, targeted pheromone and light trapping again to reduce the spread of adults. It should be noted that these methods may not be scalable under current conditions. Control of lepidopteran pest larvae currently relies on; deltamethrin (a synthetic chemical pesticide) which is used in outbreak scenarios and not suitable for use around sensitive environments, *Bacillus thuringiensis kurstaki (Btk)*, a biopesticide, or manual removal. Both pesticides are deployable at scale with many operators able to apply them but are expensive. Likewise, manual removal is feasible at scale but requires significant investment in labour costs and may not be suitable for certain areas which are inaccessible by foot. It is uncertain at what scale pheromone disruption could currently operate at in Scotland therefore feasibility assessments should be conducted to better prepare this method for deployment.

4.1.7 Case Study 3: Jewel Beetles

4.1.7.1 Introduction

This case study focuses on *Agrilus biguttatus* and *Agrilus planipennis,* two jewel beetles within the family Buprestidae, a group of phloem- and cambium-feeding insects that includes several internationally significant pests. The former is native to Europe and associated primarily with oak, while the latter, native to Asia, has become invasive in North America and parts of eastern Europe.

Agrilus beetles generally complete development over one to two years, depending on climate. Adults lay eggs in bark crevices during spring and summer. Upon hatching, larvae bore into the phloem and cambial region, creating galleries that disrupt nutrient transport. Larvae typically overwinter within host tissues and pupate in outer bark chambers prior to adult emergence.

Most *Agrilus* species are considered secondary pests, preferentially colonising stressed or declining hosts. However, under favourable climatic conditions and high population densities, some species may attack apparently healthy trees. *A. biguttatus* is closely associated with oak species, particularly pedunculate and sessile oak, which are common species in Scotland. The

species is also closely associated with acute oak decline (AOD) although research concerning this is ongoing. *A. planipennis* attacks ash species and has caused extensive mortality in invaded regions. Typical impacts on ash trees include crown thinning, epicormic shoot production, bark splitting, and progressive dieback over several years. Mortality may occur when larval densities sufficiently disrupt phloem continuity. Given the importance of oak and ash within Scottish woodlands, establishment of aggressive *Agrilus* species could have substantial ecological and economic consequences.

4.1.7.2 Affected traits under severe weather events and impact of jewel beetles

There is extremely limited evidence on the effects of wildfires on *Agrilus* species with responses likely variable, depending on whether species have evolved alongside wildfire regimes. Similarly, there is limited evidence on the effects of drought. However, there are hypothetical links which suggest drought stressed hosts may facilitate *Agrilus* outbreaks (Jones *et al.* 1992; Brown *et al.,* 2014; Rutledge *et al.*, 2017). Drought reduces host vigour, limits defensive callus formation, and may increase bark fissuring, facilitating oviposition and larval establishment. Warmer summers may further enhance voltinism and adult activity. Moderate drought is therefore likely to increase colonisation success and larval survival, particularly in stands already experiencing decline (Rutledge *et al.,* 2017; Chakraborty *et al.,* 2014).

Windthrow appears to have a slight negative effect on jewel beetle abundance. However, evidence is limited and it is uncertain what mechanism might drive this. Therefore, it should be considered that this effect may be a result of sampling error present in the individual studies. Currently UK risk assessments for *Agrilus* under extreme weather must rely on theoretical reasoning and analogues rather than direct empirical evidence.

4.1.7.3 Response, monitoring and control

With *A. planipennis* absent from Great Britain and *A. biguttatus* currently limited to central and southern England, monitoring is critical for these species. As there is limited evidence to suggest how jewel beetles will respond to severe weather events it should be highlighted here the importance of silvicultural strategies for creating woodlands that are robust to forest pests. General strategies should emphasise site-appropriate species selection and promotion of mixed stands to encourage biodiverse sites. For forestry, there should be an avoidance of extensive monocultures of susceptible hosts. Additionally, sanitation felling of heavily infested material may reduce local population build-up. Addressing knowledge gaps regarding native *Agrilus* species distribution and life history in Scotland will improve preparedness and risk assessment.

4.1.8 Case Study 4: Sap-sucking insects (e.g. Adelgid/aphids)

4.1.8.1 Introduction

Sap-feeding insects within the Hemiptera suborder Sternorrhyncha, including aphids (Aphidoidea), adelgids (Phylloxeroidea), and scale insects (Coccoidea) are insect pests that feed primarily on phloem sap using specialised mouthparts. Their life cycles typically include egg, multiple nymphal instars, and adult stages, though many species exhibit complex host-alternating cycles and parthenogenetic reproduction. Winged morphs facilitate dispersal during periods of high density or host stress.

Several species are of particular forestry relevance such as *Elatobium abietinum* and *Adelges abietis,* as these species can reach incredibly high population densities under favourable conditions. Most species are native or long established in Europe, utilising spruce, fir, hemlock, and other conifers widely planted in Scotland, as hosts.

Feeding may cause needle yellowing, premature needle loss, gall formation, honeydew deposition, and growth reduction. Severe or repeated infestations may predispose trees to secondary pathogens or contribute to decline, particularly in monoculture plantations.

4.1.8.2 Affected traits under severe weather events and impact of sap-sucking insects

There is no strong evidence for direct impacts of severe weather events on sap-sucking insect populations. Like moth defoliators they rely on living foliage however, feeding mechanisms between the two groups differ.

There are links between sap-sucking insects and drought although responses are typically non-linear. Moderate or intermittent drought may increase nitrogen concentration in foliage and reduce host defences, enhancing reproduction and survival (Kolb *et al.*, 2006, Leybourne *et al.*, 2021). Experimental studies on *E. abietinum* have demonstrated increased reproductive rates under moderate water stress, whereas continuous severe drought reduces survival (Banfield, Zanin & Leather, 2014).

Higher temperatures may enhance overwinter survival, compounding effects of moderate drought. However, extreme or prolonged drought may suppress populations through host deterioration. Stage-specific responses occur in some adelgids, where drought may benefit free-feeding stages, but inhibit gall development, which requires actively growing tissues.

4.1.8.3 Response, monitoring and control

Managing sap-sucking pests is inherently difficult as their small size and waxy coatings provide natural defences alongside their feeding sites being relatively hidden. These issues are compounded in mature forest stands where conventional chemical control becomes unfeasible due to the scale required. In their native ranges, natural enemies such as predators and parasitoids, tend to keep sap-sucking insect populations in check and below damaging levels. As with many insect pests, outbreak years can occur when climate or site conditions become favourable leading to increased levels of damage for which management options are limited (Day *et al.*, 1998). Therefore, pro-active management should include promoting natural predators and parasitoids in Scottish Forests, for example by increasing habitat diversity (e.g., maintaining hedges, ground cover and mixed-species forests).

4.2 Recommendations

The limited data available makes concrete recommendations difficult. However, there are some logical conclusions from this synthesis that may help land managers to adapt to incoming changes to their landscapes.

For wildfires, increasing our preparedness should be paramount. Whilst effects between species of bark beetles were seen to vary, there is no synthesis of which species present in Scotland that have evolved alongside wildfires and which have not. Management responses are likely to differ depending on this information, as species that have evolved alongside

wildfires may require more rapid intervention than those that have not. Combining this knowledge with detailed distribution maps will support local decision-making by land managers. Intervention will likely involve thinning or sanitation felling in weakened stands to reduce breeding material.

Drought events will likely need two major interventions to reduce defoliator larvae fitness benefits. Firstly, timely application of pesticides/biocontrol to reduce larval growth and reduce damage to any hosts. Secondly, a higher effort of pheromone mating disruption and trapping, as adults begin to emerge, to counter any increased dispersal and breeding capabilities. This could reduce the likelihood of an outbreak year, although these interventions applied in this manner have not been formally tested.

Windthrow management responses for bark beetles should largely look at removing windthrown trees where possible. This is usually a significant task with limited resources so the priority should be to remove wind-damaged material in high-risk areas, such as forests near ports. Areas where beetle activity is likely to be highest, such as stand edges or storm gaps, uprooted or wind-broken trees, should be prioritised. This is particularly important to reduce the risk for establishment of *I. typographus*. This pest poses a particular high risk under future severe weather, considering the ability to shift to primary pest behaviour under favourable conditions, although the risk for establishment in Scotland is currently considered low. Higher temperatures can directly impact development rates and phenology (earlier spring flight, increased voltinism) while drought and storm events can provide a surplus of suitable breeding material. This combination could allow this species to cause substantial economic damage if it was to establish in Great Britain in the future. Principal UK forestry species at risk are Norway spruce, as the primary host, and Sitka spruce which has recently been confirmed as a suitable host (Inward *et al.*, 2025).

It is important to note that large, same -age monocultures, such as extensive Sitka spruce stands that characterise much of Scotland's commercial forestry landscape, are generally more vulnerable to pest outbreaks and wind damage than forests with greater species and age diversity. Mixed species forests are more resistant to natural disturbances such as windstorms (Jactel *et al.*, 2017).

Ultimately, as our understanding of how these species may react is still limited, our ability to manage forestry pests will be reactive in many cases. The most proactive recommendations that can be suggested here would be, for Scotland to maintain its robust biosecurity strategy to prevent further incursion of forest pests avoiding the need for further control costs. Additionally, when considering future woodland creation, restoration and management, avoiding large monocultures and encouraging diverse woodlands should be at the forefront of this thinking. These attributes will support ecosystem functions such as pest control by natural enemies by providing an array of habitats for predators and parasitoids. It will also reduce the probability of pest species establishing and spreading by breaking up susceptible landscapes.

4.3 Knowledge gaps

Whilst not the primary aim of this work, several important knowledge gaps were identified. There is a lack of evidence globally on how many forestry pest species respond to severe weather events, limiting our ability to predict future impacts in Scotland. The main reason for this is likely due to the challenging logistics of setting up appropriate experimental designs to capture data pre and post severe weather event.

Recommendations arising from this project fall within three areas:

a. Utilising existing data

- Review existing datasets and monitoring programmes to identify opportunities for assessing pest responses to past storms, droughts, wildfires, and floods.
- Review forest pest species present in Scotland to identify those associated with disturbance regimes such as wildfire, which may indicate species likely to benefit from future wildfire events.

b. Improving monitoring and surveillance

- Ensure standardisation of survey methods, trapping protocols, sampling intervals, and measures of pest abundance or damage severity to improve comparability across sites and years.
- Consider incorporating additional species (e.g. other pests and pathogens) into routine surveillance, specifically those that are common, quick to assess, and easy to quantify. These species could act as an indicator species and serve as a proxy for broader ecological responses.

c. Targeted research

- Targeted monitoring following severe weather events and along disturbance gradients to better understand short- and long-term pest responses.
- Conduct controlled drought experiments, such as glasshouse studies, to improve understanding of species responses to water stress and validate current findings.
- Undertake experimental studies examining interactions between tree stress, pests, and secondary pest or pathogen attack.
- Where appropriate, use experimental felling studies to simulate windthrow and assess responses of different beetle groups, including species with contrasting strategies such as *Agrilus* and *Ips*.

Together, these actions would improve understanding of how forest pests respond to severe weather events and strengthen our ability to predict future risks under a changing climate.

5 Conclusion

Understanding how plant pests will respond to severe weather events is vital for informing future management and creating resilient forests and plantations. Individual studies are difficult to use as an evidence base due to the variable response species show to severe weather events resulting in unclear priorities for land managers and policy makers. In this review, we highlight the current available evidence for how different feeding guilds of forest invertebrate pest species respond to severe weather events. We also conduct statistical analysis of this evidence to better understand true effects across multiple studies.

This work shows that severe weather events can impact the biology and ecology of forestry pests, and depending on the severe weather event, these impacts can be either positive or negative and vary dramatically in scale. These findings also underscore the complexity of forest ecosystems and the challenges in understanding how forest invertebrates will respond to severe weather events which are predicted to become more frequent over the next decade and beyond. Although sample sizes for this work are small, we believe the results corroborate long held hypothesise of how certain groups will respond to severe weather events. This lets us provide preliminary management suggestions that are likely to yield benefits Scottish forests and woodlands. Nevertheless, it is clear forest ecosystems are becoming more complex with varying tree species compositions, more pest species, increased severe weather event frequency, and changing management priorities. It would likely benefit land managers, foresters, and policymakers to better understand these dynamics, to allow for more concrete and focused management decision making, to ensure Scottish forest management remains evidence-based and equitable.

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Appendix

Appendix 1: CABI compendium case study species lists.

Species	Common name	Impact	Distribution	UK	Host species
Ips avulvus	Southern pine engraver	Mostly a secondary pest of pines older than 4–5 years that are weakened, under favourable conditions (severe drought) populations can become epidemic	North America	No	*Pinus* spp.
Ips calligraphus	Six-spined Ips	Mostly secondary bark beetle of pines that can kill stressed trees	North America, China	No	*Pinus* spp.
Ips cembrae	Large larch bark beetle	Mainly a secondary pest of larch, usually breeds in freshly cut logs, wind-thrown stems, storm-damaged or dying trees	Europe, Russia	**Yes**	Larch (*Larix* spp.)
Ips grandicollis	Five-spined bark beetle	Secondary bark beetle of pines that can kill weakened trees and small trees, prefers recently felled trees and slash, but it can infest stressed or weakened living pine	North America, Australia, China	No	*Pinus* spp.
Ips pini	Pine engraver	Primarily breeds in fresh logging slash, storm-thrown trees, and damaged or drought-stressed pines; when populations build up it can also attack and kill standing trees with reduced vigor	North America	No	*Pinus* spp.
Ips typographus	European spruce bark beetle	Normally breeds in wind-thrown, storm-damaged, drought-stressed or recently felled trees, but when populations build up, mass attacks overwhelm defenses and kill apparently healthy older spruce stands. Large outbreaks have caused extensive spruce mortality and economic losses in Central and Northern Europe, especially after storms and droughts	Eurasia	**Yes (not established)**	Norway spruce (*Picea abies*)
Pityogenes chalcographus	Six-toothed spruce bark beetle	Secondary pest to already compromised hosts, but population build-up (often after *I.typographus* outbreaks) enable attacks on vigorous trees	Eurasia	**Yes**	Norway spruce (*Picea abies*), other conifers: *Abies* spp., *Larix* spp., *Picea* spp., *Pinus* spp., *Pseudotsuga* spp., *Tsuga* spp.

Figure 8: CABI compendium species list for bark beetles (CABI, n.d.a).

Species	Common Name	Impact	Distribution	UK	Tree Hosts
Dendroctonus ponderosae	Mountain Pine Beetle	Secondary pest of weakend trees & beetles introduce blue-stain fungi, eventual tree decline and mortality Can become a primary pest attacking live trees under epidemic phase	Eastern North America	No	*Pinus* spp.
Dendroctonus pseudotsugae	Douglas-fir beetle	Secondary pest of weakend trees & beetles introduce associated fungi, eventual tree decline and mortality Can become a primary pest attacking live trees under epidemic phase	Eastern North America	No	Douglas fir (*Pseudotsuga menziesii*)
Dendroctonus valens	Red turpentine beetle	Secondary pest in native range- large reddish-white pitch tubes, these attacks generally only kill weakened individuals or remain sublethal However is a primary pest in invasive range	North America, Parts of central and western China	No	*Pinus* spp.
Dendroctonus micans	Great spruce bark beetle	Primary pest that attacks living, often apparently healthy spruce. If populations escape natural control, numbers can build up aleading to stem girdling and large-scale mortality	Europe, Eastern Siberia, Northern Japan and China	**Yes**	*Picea* spp.

Figure 9: CABI compendium species list for bark beetles (CABI, n.d.b).

Species	Common name	Impact	Global Distribution	UK	Tree hosts
Agrilus anxius	Bronze birch borer	Causes crown thinning, branch dieback, and death of stressed birch trees.	Native to North America.	No	Birch (*Betula* spp.).
Agrilus biguttatus	Oak splendour beetle	Contributes to oak decline; bark cracking, canopy dieback, and exit holes on trunks.	Europe and western Asia.	Yes	Oak (*Quercus* spp.)
Agrilus bilineatus	Two-lined chestnut borer	Branch wilt, canopy thinning, and eventual death in infested trees.	Native to North America.	No	Oak (*Quercus* spp.), chestnut (*Castanea* spp.).
Agrilus fleischeri	Elm borer	Causes branch dieback and tree death, similar to symptoms of Dutch elm disease.	Native to East Asia	No	Elm (*Ulmus* spp.).
Agrilus planipennis	Emerald ash borer	Rapid crown dieback and death within 2-4 years; bark splitting and D-shaped emergence holes.	Native to East Asia; invasive in North America and Europe.	No	Ash (*Fraxinus* spp.)
Agrilus sinuatus	Hawthorn jewel beetle	Causes dieback in hawthorn; infested branches wilt and die, especially in old trees.	Europe	Yes	Hawthorn (*Crataegus* spp.), apple (*Malus* spp.)

Figure 10: CABI compendium species list for jewel beetles (CABI, n.d.c).

Species	Common name	Impact	Global Distribution	UK	Tree hosts
Adelges abietis	Eastern spruce gall aphid	Gall forming adelgid; distinctive pineapple shaped galls on spruce shoots.	Widely recorded in Europe	**Yes**	Norway spruce (*Picea abies*) and Sitka spruce (*Picea sitchensis*).
Adelges tsugae	Hemlock woolly adelgid	Sap sucking adelgid forming white woolly masses on hemlock twigs; can cause decline and mortality of hemlock.	Native to Asia; introduced and invasive in eastern North America	No	Hemlocks (*Tsuga* spp.); spruce (*Picea* spp.) used as secondary host
Cinara costata	Mealy spruce aphid	Large, wax covered (mealy) aphid on spruce stems and branches.	Recorded across parts of Europe	**Yes**	Spruce (*Picea* spp.)
Elatobium abietinum	Green spruce aphid	Important defoliating aphid of spruce; feeds on needles and can cause severe needle loss and growth reduction.	Native to continental Europe	**Yes**	Spruce species (*Picea* spp.), especially Sitka spruce (*Picea sitchensis*).
Physokermes hemicryphus	Small spruce bud scale	Soft scale insect; females are rounded, brown and immobile on twigs and at bases of buds.	Recorded in Europe	**Yes**	Spruce (*Picea* spp.), particularly Norway and Sitka.
Physokermes inopinatus	Hungarian spruce bud scale	Feeds on the sap from the needles - secondary issues caused by honeydew leading to sooty mold	Recorded in Europe	No	Abies sp, Picea spp.
Physokermes piceae	Spruce bud scale	Discoloration and drying of needles, drying of branches and even whole plants. Secondary issues caused by honeydew leading to sooty mold	Recorded in Europe	No	*Abies* sp, *Picea* spp.
Pineus pini	Scots pine adelgid	Woolly adelgid on pines; feeds at bases of needles and on shoots.	Widely recorded in Europe	**Yes**	Scots pine (*Pinus sylvestris*)

Figure 11: CABI compendium species list for sap-sucking insects (CABI, n.d.d).

Appendix 2: Species list from meta-analysis

Table 1: List of species included in the meta-analysis.

Pest species	Pest Order	Pest Family	Feeding guild
Agrilus obscuricollis	Coleoptera	Buprestidae	Bark beetle
Agrilus viridis	Coleoptera	Buprestidae	Bark beetle
Agrilus sulcicollis	Coleoptera	Buprestidae	Bark beetle
Agrilus angustulus	Coleoptera	Buprestidae	Bark beetle
Dendroctonus simplex	Coleoptera	Curculionidae	Bark beetle
Dendroctonus rufipennis	Coleoptera	Curculionidae	Bark beetle
Dendroctonus valens	Coleoptera	Curculionidae	Bark beetle
Dendroctonus terebrans	Coleoptera	Curculionidae	Bark beetle
Ips pini	Coleoptera	Curculionidae	Bark beetle
Ips peroti	Coleoptera	Curculionidae	Bark beetle
Ips grandicollis	Coleoptera	Curculionidae	Bark beetle
Ips calligraphus	Coleoptera	Curculionidae	Bark beetle
Ips avulsus	Coleoptera	Curculionidae	Bark beetle
Thaumetopea pityocampa	Lepidoptera	Notodontidae	Leaf defoliator
Thaumetopea pityocampa	Lepidoptera	Notodontidae	Leaf defoliator
Choristoneura fumiferana	Lepidoptera	Tortricidae	Leaf defoliator
Choristoneura fumiferana	Lepidoptera	Tortricidae	Leaf defoliator

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