



A Systematic Review of the Effects of Multi-purpose Forest Management Practices on the Breeding Success of Forest Birds

João M. Cordeiro Pereira¹ · Grzegorz Mikusiński² · Ilse Storch¹

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Abstract

Purpose of Review We aimed to summarize the evidence linking multi-purpose forest management (MPF) to bird nesting and fledging success in temperate and boreal forests and to identify outstanding research gaps. Forest birds are in decline worldwide, but an ongoing move from production-oriented management towards MPF, integrating biodiversity conservation with other uses, may help counteracting these trends. The effects of MPF on bird diversity and abundance are well-studied, but less is known about effects on bird demographics.

Recent Findings We retrieved 101 studies, reporting 342 outcomes of MPF for nesting and fledging success. Due to the heterogeneity of the studies, we opted for a systematic mapping approach, accompanied by vote-counting and narrative review. Studies covered 11 types of MPF and 151 bird species. The most frequently studied interventions were overstorey retention and prescribed burning, but research was markedly biased towards temperate North America. Most outcomes (79.5%) were non-significant, and studies often found that breeding success was driven by ecological processes at both broader and finer scales than management interventions. Thus, managing for breeding success likely requires complementary management actions at various scales. Nonetheless, significant positive and negative outcomes of MPF were also found, inclusively affecting species of conservation concern, highlighting the variability and context-dependence of MPF effects.

Summary In order to foster effectiveness of MPF for forest birds, future research should focus on a set of under-researched interventions and regions, as well as on ecosystem-wide experiments accounting for functional links between bird abundance, demographics, nest predation, and food supply.

Keywords Nesting success · Fledging success · Nest predation · Evidence-based conservation · Systematic mapping

Introduction

Close to 31% of the global terrestrial surface is covered by forests, encompassing most of the worlds' terrestrial biodiversity, and nearly half of that area consists of boreal and temperate forests [1]. Forest intactness is declining worldwide [2], as are the populations of forest-dependent species [3], including birds [4], the most closely monitored taxonomic group [5]. Abundance of boreal forest breeding birds has declined by more than 30% since 1970 in North America

[6] and by 20% since 1980 in Europe [7], mostly due to the combined effects of climate change and rapid expansion of intensive forestry [8, 9]. In the temperate zone, declines are not as strong [6, 7], but a long history of human settlement and forest use has left little intact forest [10], and intensification of timber extraction still plays a role in driving bird declines [11, 12]. Thus, a shift in forest management practices in temperate and boreal forests may contribute to revert such declines.

Production-oriented silviculture is characterized by a simplification of forest structure, leading to loss of biodiversity by filtering out taxa dependent on late-successional structures or naturally-disturbed areas [13–15]. One option to address this issue is to set aside areas of forest for natural development. This segregative approach is uniquely beneficial to biodiversity if applied at large spatial scales [16, 17]. In addition, there is increasing societal interest in multi-purpose forest management (MPF) approaches, also designated

✉ João M. Cordeiro Pereira
joao.cordeiro.pereira@wildlife.uni-freiburg.de

¹ Chair of Wildlife Ecology and Management, University of Freiburg, Tennenbacher Str. 4, 79106 Freiburg, Germany

² School for Forest Management, Swedish University of Agricultural Sciences, Box 43, 739 21 Skinnkatteberg, Sweden

multi-functional, integrative [18], ecologically sustainable [19] or closer-to-nature forest management (as per EU Forest Strategy for 2030, [20, 21]). MPF is defined as a set of practices that enable the provision of wood products alongside other services, including biodiversity conservation, by restoring and maintaining forest ecosystem integrity [18, 19]. It encompasses a broad array of practices, such as retention forestry [22], close-to-nature forestry [23], structural complexity enhancement [24], and natural disturbance-based forest management [25•], with a common denominator of bridging the biodiversity gap between fully-protected and intensively-managed forests [26]. Especially in the temperate zone, where old-growth forests are rare and would take a long time to develop, MPF practices are an attractive option for conservation [16].

MPF practices have proven effective at increasing structural complexity of production forests [27, 28]. In several European countries, the implementation of close-to-nature forestry in recent decades is thought to explain a reversal in the negative trends of forest bird populations [29–31]. Nonetheless, no form of MPF has an univocally positive effect on bird abundance and diversity, but outcomes rather vary across species and functional groups [32, 33]. Thus, the implementation of multiple MPF types is likely necessary to boost bird diversity at the landscape scale [34, 35]. For instance, species dependent on mature forests respond positively to retention of large living trees, tree patches and snags following harvesting [32, 36], whereas several specialized woodpeckers and ground or shrub-foraging species benefit from the creation of open forest conditions, as through prescribed burns [37, 38]. However, most aforementioned research focuses on the responses of bird assemblages to MPF in terms of abundance, species richness, and composition, which do not necessarily reflect habitat quality [39]. In order to achieve its conservation goals, management should strive not only to create habitat where targeted species are temporarily abundant but also to create high-quality habitat, enabling those species' long-term persistence [40].

Demographic parameters—e.g. annual adult survival, clutch size or nesting success—determine the long-term stability of bird populations, providing as a whole a better measure of habitat quality than short-term abundance responses [40, 41•]. Unfortunately, as highlighted by [42, 43] in their reviews of birds' responses to timber management and restoration plantings, very few studies have examined demographic responses. Nonetheless, there is evidence of standard forestry practices affecting nesting success (e.g. [44, 45]), potentially creating demographic sinks [46••]. Consequently, evaluating the effectiveness of MPF practices for bird conservation in a comprehensive manner implies measuring their demographic outcomes. Additionally, these data can inform predictive models of population dynamics under multiple management scenarios (e.g. [47, 48]), help

in prioritization of conservation areas (as in [49]), and allow for detection of ecological traps (e.g. [50, 51]), i.e. situations where abundance of a species is decoupled from habitat quality, due to a low-quality habitat attracting individuals [39]. Ecological traps are a risk especially in novel habitats, such as those created by silvicultural management [52, 53].

Among bird demographic parameters, nesting success—the probability that at least one chick fledges from a nest [54]—is fairly easy to estimate and hence the most commonly evaluated [55, 56]. Alongside it, a more detailed metric, fledging success—expressed either as number of fledglings or proportion of eggs resulting in fledged young—is also often measured. Both metrics represent a sensitive point in the annual cycle of forest-breeding birds, since nestling growth is highly energy-demanding [57], and rates of nest loss, especially in passerines, can be very high [58], thus conditioning recruitment for the following breeding season [59, 60]. These demographic metrics may be affected jointly by multiple factors [61], such as food availability for nestlings [62], nest predation [63], parasitism [64] or brood parasitism [65]. However, it is nest predation that assumes a prominent role in limiting nesting success, particularly for open-cup nesters [63]. Direct control or exclusion of nest predators has proven an effective tool to boost populations of many bird species [66–68]. On the other hand, fledging success can be strongly influenced by weather conditions, food availability and interactions of the two—individual nestlings are susceptible to starvation, as demonstrated in studies carrying out experimental food supplementation [57, 62], or observing phenological mismatches with food supply (e.g. [69]). Therefore, measuring nesting and fledging success is helpful to narrow down the ecological drivers of changes in bird population size, so management can be adjusted to directly address those drivers [70, 71].

The effects of forest structure on nest predation and, thus on nesting success, have been thoroughly investigated using artificial nests [72], although this method precludes conclusions about species-specific predator–prey interactions [73, 74]. Timber harvests were for long hypothesized to increase nest predation, both due to creation of habitat edges at the stand scale and fragmentation of forests at the landscape scale [75], but it is yet unclear if partial harvesting, a form of MPF, could produce similar outcomes. Multiple artificial-nest studies have even found nest predation to increase towards the forest interior [76, 77]. On the other hand, wherever MPF promotes more complex vegetation, this may reduce nest predation by ensuring improved nest concealment (e.g. [44]). As for the effects of MPF on nestling food supply, studies have shown negative effects of partial harvesting on food provisioning rates for some species (e.g. [78]), but no effect on food abundance for others (e.g. [79]), and prescribed burns reportedly increase abundance of spiders [80•], a key prey item for songbirds [81, 82].

Still, it is unclear whether changes in food supply due to MPF practices translate into increased fledging success in contrast to intensively-managed stands. A growing body of evidence reveals declines in forest insect populations [83, 84], but such declines may be countered by increasing forest structural complexity [83] and favouring native plant species [85], with potential benefits for birds. Clearly, more evidence is needed from studies explicitly linking management practices with demographic outcomes and their drivers, especially through experimental approaches [43, 86, 87].

In this paper, we review the current evidence linking MPF practices in boreal and temperate forests to bird demographics, focusing on nesting and fledging success, and aiming to answer the following questions: (1) Do MPF practices result in improved nesting or fledging success outcomes for forest birds, when compared with more production-oriented management or with natural benchmarks? (2) How do outcomes vary across different forms of MPF? (3) What implications does this have for assessing habitat quality in MPF treatments? (4) Which research gaps exist, regarding regions, management interventions, experimental designs and species covered? With this we strive not only to offer a summary of the available evidence, but also provide directions for further research, ultimately aiming to strengthen evidence-based management towards the conservation of forest birds.

Methods

Inclusion Criteria

For screening of studies resulting from database searches, we defined an a priori set of inclusion criteria, described below. We followed the PICO (Population-Intervention-Control-Outcome) framework, adapted from evidence-based medicine methodology [88, 89].

The population of interest consisted of studies on forest-inhabiting breeding birds conducted in boreal and temperate forests on either hemisphere, including peer-reviewed studies as well as the grey literature they may cite. We included four biomes [90]—(1) boreal forests/taiga, (2) temperate broadleaf and mixed forests, (3) temperate coniferous forests and (4) Mediterranean forests, woodland and scrub—but also any smaller forest patches (e.g. riparian corridors) in neighbouring drier biomes (deserts or temperate grasslands and savannas). We defined forests as per FAO [91], thus including early-successional areas with potential to develop into forest. Studies may focus on one or more bird species, of which at least one must be a forest bird species, understood as nesting and foraging more than incidentally in forests over a significant portion of its range [33].

The treatments of interest were MPF interventions. We only included interventions modifying stand-scale forest

structure and which are expected to offer a benefit for biodiversity when compared with production-oriented forestry, even if biodiversity conservation was not the primary management goal. This included direct interventions, e.g. creating canopy gaps by harvesting, but also indirect interventions, e.g. exclusion from ungulate browsing, and passive interventions, e.g. avoiding thinning of understorey vegetation. Conversely, we excluded clearcutting (when compared against unharvested forests), control of silvicultural insect pests, direct control of nest predators, food supplementation, provision of nest boxes, modifications of landscape-level forest amount or configuration, and conversion of non-forest land to forest. We only included studies with experimental or quasi-experimental designs, i.e. where management interventions were treated categorically, controls were available, and treatment effects were separable from other measured covariates. So-called “natural experiments” (e.g. wildfires, storms, insect outbreaks) were excluded, as they may differ in their effects from anthropogenic modifications [50].

MPF interventions may be compared both against more production-oriented, “business-as-usual” management practices, or against stands that represent a target state or benchmark. We named these as alternative management (AM) and natural reference (NR) controls, respectively. Whereas the former provide information on the actual impact of MPF interventions, the latter inform how closely that impact approaches a desired scenario [92••]. NR controls are not necessarily unmanaged forests but must not have been recently subjected to the MPF intervention or its more intensive alternative. The choice of which stand types are designated as AM or NR controls depends on the type of management intervention under study and is described in detail in Table 1.

Lastly, we included studies reporting on two response variables—nesting success and fledging success, as defined in the “Introduction” section. Studies must have conducted a statistical test of the difference in these parameters between the treatment and control. Other demographic parameters, such as clutch size or annual adult survival, did not fall under the scope of this review. Nesting or fledging success measurements may have been obtained from natural nests or nest boxes, but we excluded studies using artificial eggs or quail eggs.

Database Search and Article Screening

We built one search string with 39 terms, having in mind the scope and inclusion criteria of this review: (**bird* OR avian*) AND (*forest* OR woodland**) AND (*experiment* OR manipulat* OR remov* OR reduct* OR control* OR addit* OR supplement* OR creat* OR enrich* OR retain* OR promot* OR restor* OR improv* OR conserv* OR manag* OR prescrib* OR legac* OR treatment OR intervention OR*

Table 1 Description of 11 MPF classes into which we grouped the reviewed studies, including the conservation goals associated with these management types and a description of the experimental controls applicable to each (alternative management control, AM, or natural reference control, NR)

MPF intervention class (no. of studies)	Description	Conservation goals	AM control	NR control
<i>Retaining overstorey</i> (37 studies)	Retention of overstorey components—single trees, tree patches and/or strips—in the course of tree harvesting operations, including shelterwood cuts and conversion from even-aged to two-aged or single-tree selection harvests	In landscapes dominated by even-aged stands and clearcutting, retention practices aim to ensure ecosystem continuity across harvesting cycles (“lifeboating”), thereby limiting negative impacts on species reliant on mature, closed-canopy forest [22], whilst also creating more heterogeneous, uneven-aged forest stands, on which many forest specialists depend [23]	Stands with higher intensity of harvesting (often recent clearcuts), or regenerated even-aged stands following clearcutting	Unharvested forest, at least as old as one harvesting rotation interval
<i>Restoring fire</i> (19 studies)	Use of prescribed burns to emulate a natural disturbance regime, which may involve burning applied with a specific frequency, extent and seasonality (e.g. growing-season burns) and may be complemented by thinning operations	In landscapes with historically-suppressed natural disturbance regimes, on which fires had originally played an important role [109], prescribed burning aims at recreating and maintaining open-canopy or savanna conditions, hence benefitting taxa that are dependent on semi-open habitat, many of which are of conservation concern [110, 111]	Stands either with a history of fire suppression or of prescribed burns that deviate from a natural disturbance regime in their frequency, extent or seasonality (e.g. dormant-season burns), resulting in a more limited impact	Stands in unmanaged reserves, naturally disturbed by fire or other agents (e.g. insect outbreaks), or otherwise closer to a natural disturbance regime
<i>Thinning overstorey</i> (13 studies)	Use of mechanical thinning of the overstorey to emulate a natural disturbance regime, often as a surrogate for fire	Same as above, for restoring fire	Same as above, for restoring fire	Same as above, for restoring fire
<i>Retaining understorey</i> (10 studies)	Refraining from high-intensity thinning of forest understorey, particularly with herbicide use; alternatively, protecting the understorey from high levels of browsing or grazing (e.g. through fencing or diversionary feeding)	Understorey retention aims to counter the potentially negative effects of high-intensity thinning (e.g. for biomass harvests, [112]), excessive browsing [113] or grazing [114] on forest taxa dependent on this vegetation layer	Stands subjected to a higher intensity of thinning through mechanical or chemical means, or to a higher intensity of grazing/browsing	Stands where understorey has not been thinned, or has been left ungrazed or with low-intensity browsing for significantly longer than in MPF treatment
<i>Thinning understorey</i> (5 studies)	Partial clearing of understorey vegetation, including removal of non-native shrub species	Understorey thinning aims to benefit taxa dependent on a lightly-disturbed understorey layer, otherwise absent due to encroachment by non-native vegetation (e.g. [115]), fire suppression or absence of natural browsing/grazing [116]	Stands with denser understorey than expected in the presence of natural disturbances, or invaded by non-native shrub species	Stands with a naturally-disturbed understorey, or which have not been invaded by non-native shrub species

Table 1 (continued)

MPF intervention class (no. of studies)	Description	Conservation goals	AM control	NR control
<i>Restoring tree species composition</i> (5 studies)	Converting stands to a more natural and site-adapted tree species composition, by favouring native species or species with a lower production value (e.g. due to slow growth)	In managed forest landscapes where forestry has favoured certain tree species (often forming monocultures), it is expected that restoring a more natural, site-adapted species composition will increase the biodiversity value of forests and their resilience in the face of changing disturbance regimes [23]	Stands dominated by one or more species that are favoured for their production value, of comparable age to MPF treatment	Stands with a natural tree species composition, of comparable age to MPF treatment
<i>Salvage with retention</i> (4 studies)	Retention of living trees and snags in the context of salvage logging operations, following major disturbances (wildfires, windthrows or insect outbreaks)	Salvage logging negatively affects various taxa reliant on heavily-disturbed forests, and retention practices have the potential to limit that impact [117]	Fully salvage-logged stands, or otherwise more intensively logged than the MPF treatment	Stands that remain unlogged following a major disturbance
<i>Buffering edges</i> (3 studies)	Creating a more complex shrubby ecotone on forest edges (including clearcut edges), through border-edge cuts, planting or passive means	More complex and gradual edge habitats are expected to be of higher quality for birds than the abrupt edges typically found in fragmented landscapes [118]	Abrupt forest edges	Gradual forest edges formed by natural disturbances or edaphic/hydrological conditions
<i>Restoring hydrology</i> (2 studies)	Restoring a natural flooding regime in alluvial or peatland forests, by blocking artificial drainage systems or removing dams and berms	These interventions aim to revert, at least partially, the impacts of forest drainage and stream regularization on ecosystem dynamics [119], and consequently improve habitat quality for species reliant on high water tables or regular episodes of flooding (e.g. [120])	Alluvial or peatland forests in which flooding has been suppressed by drainage or damming	Unmanaged stands, subjected to unaltered flooding regimes
<i>Creating dead wood</i> (1 study)	Active creation of snags in production forests, by mechanical means (e.g. topping certain trees during harvesting)	Structural complexity enhancement, such as by actively creating dead wood, aims at accelerating the development of late-successional features in production stands, thereby creating habitat for taxa that are otherwise dependent on old-growth forests [24]	Clearcut stands, which may contain retained or created snags at a lower density and/or with a more dispersed distribution than in the MPF treatment	Stands with high amounts of naturally-formed dead wood
<i>Others</i> (7 studies)	Interventions that cannot be attributed to any of the categories above, as they affect multiple forest layers and combine multiple tools (e.g. grazing and selective thinning, [121])	Variable	Variable	Variable

retention OR silvicult) AND (food* OR feed* OR forag* OR predat* OR “nest* site*” OR “nest supply” OR “nest availability”) AND (“nest* success” OR “breeding success” OR productiv* OR fledg*ing* OR offspring OR survival)*. MPF is a term with very broad definitions, and many relevant studies do not include it in their title, abstract or keywords. Likewise, terminology about individual MPF practices is varied and often inconsistent. For this reason, instead of including “multi-purpose forest management” or any specific practice in our search string, we used a set of verbs which maximizes search sensitivity whilst sacrificing specificity, as suggested by [93]. Furthermore, we did not include geographical terms in our search string, but filtered out studies outside of temperate and boreal biomes during the subsequent screening process.

Using the aforementioned search string, we ran a topic search (i.e. title, abstract and keywords) on the Web of Science Core Collection and eight other Web of Science databases (BIOSIS Citation Index, BIOSIS Previews, Current Contents Connect, Data Citation Index, KCI-Korean Journal Database, Russian Science Citation Index, SciELO Citation Index and Zoological Record), on 15 December 2021. We searched for additional studies on the Conservation Evidence database (<https://www.conservationevidence.com/data/studies>), which was purposefully built to gather evidence about the effectiveness of management actions [94], on 15 June 2022. We filtered the search on Conservation Evidence using the following criteria: category “Forest” or “Birds”; habitat “Forest & Woodland”; threat “Natural systems modification”, “Biological resource use” or “Other”; action type “Land/water management”, “Land/water protection”, “Species management” or “Other”. We applied no filters for keywords or countries. Searches on both databases were repeated once more on 22 November 2023, to capture recently published studies.

After removing duplicate results, search hits were then screened against the inclusion criteria, first by reading the title, then the abstract or summary, and when necessary by reading the full text. Each of these steps resulted in a portion of the search hits being excluded, until we reached a set of relevant studies. Whenever there was doubt about whether to exclude a study based on the title or abstract, we adopted a conservative approach and retained it for the next step of screening. Lastly, we expanded that set of studies by screening all studies citing them in the Web of Science Core Collection (forward search), as well by screening their bibliographies (backward search), and adding any relevant hits. This citation-based search method (“citation chasing” or “snowballing”), though not widely in use, is recommended to supplement a database search [95, 96], and it provided us with relevant grey literature which is not captured by Web of Science searches. Citation chasing is especially effective at detecting semantically-connected studies when the topic of

interest contains inconsistent terminology [95, 97], as is our case. When we found more than one study on the same study area and species, with overlapping datasets, we kept only the study with the largest dataset. The full screening workflow, with the number of publications considered on each step, is presented on Fig. 1, as a PRISMA flowchart [98], designed with R package “DiagrammeR” [99, 100].

Data Extraction and Summarization

We analysed studies following a systematic mapping approach [101, 102], which prioritizes building a comprehensive summary of the state of evidence, knowledge gaps and knowledge clusters in a broad topic of interest—as are different management actions and their effects on forest birds (e.g. [92••])—over a purely quantitative analysis of a narrower set of studies. From each study, we extracted all bibliographical information and study area coordinates, which we assigned to the biomes defined by [90]. As a taxonomy is lacking for MPF interventions, we classified the interventions analysed in each study using an ad hoc approach, based on their conservation goals, on which vegetation layers were most affected and which tools were employed (e.g. harvesting or fire). We provide a description of each of these classes on Table 1. Based on the intervention under study, we checked which type of control was used (AM, NR or both) and which experimental design the study followed—before-after (BA), control-impact (CI) or with both comparisons (BACI).

Next, we extracted all relevant outcomes reported in each study. Each study may contain multiple outcomes, defined as the response of a single bird species or an aggregate of species to a given MPF intervention in comparison with a given control (AM or NR), measured by a given response type (fledging or nesting success). For each outcome, we noted if the outcome of the MPF practice was statistically significant (at $\alpha = 0.05$), and if significant we noted the direction of the effect. We then obtained the frequencies of non-significant, negative and positive reported effects for each MPF intervention type, grouping them by control type and response type, and plotted these summaries with R and package “ggplot2” [103]. We opted for this vote-counting approach to summarize study outcomes, rather than for a meta-analysis, because studies were very heterogenous in nature, including several understudied management types, and did not always report the necessary data for a meta-analysis (as in [92••]). However, vote-counts do not take into account variations in sampling effort and overall study validity across studies [95]. In order to carry out a critical appraisal of study outcomes, in particular identifying whether non-significant effects may be explained by lack of statistical power, we extracted for each outcome a metric of sampling effort—the number of monitored nests per year and per treatment. The literature

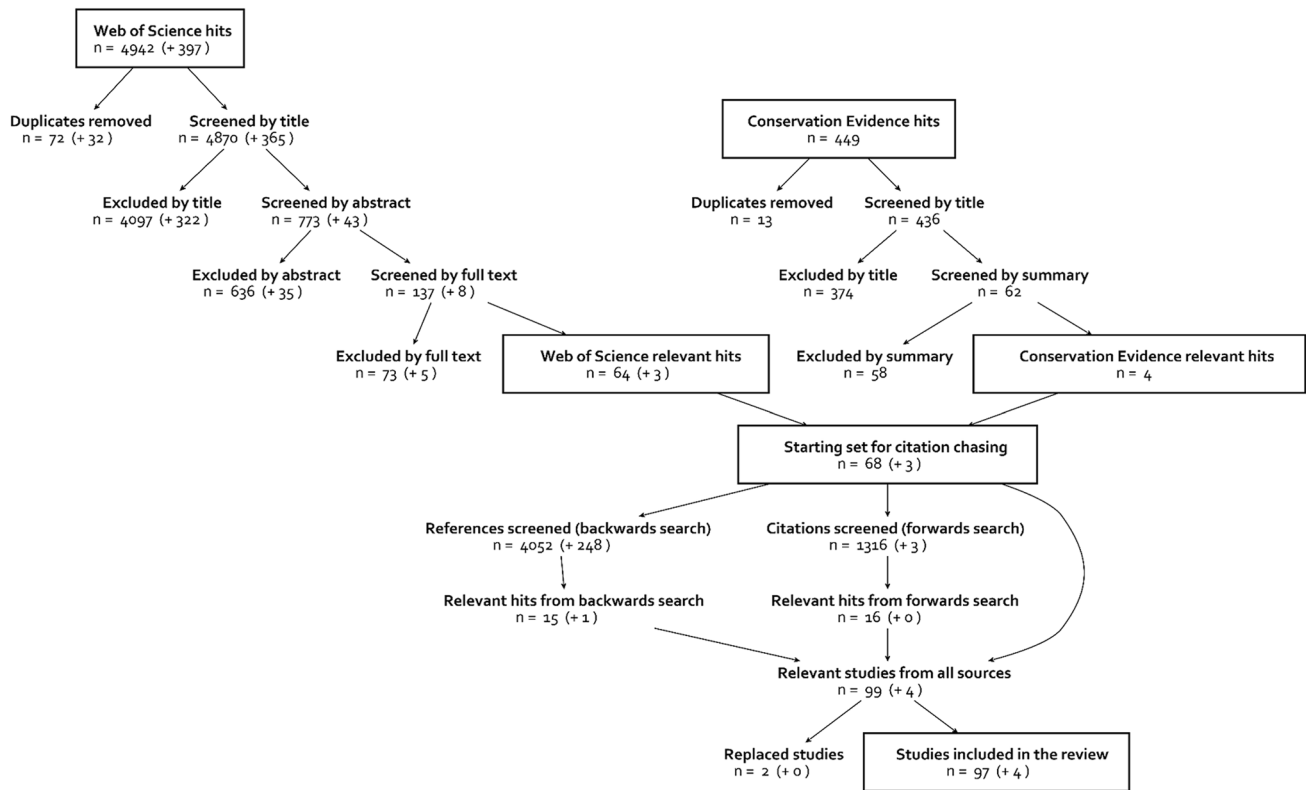


Fig. 1 Literature screening workflow, indicating numbers of studies identified, excluded and retained at each step (drawn with R package “DiagrammeR” [100]). Numbers in brackets refer to follow-up search on 22 November 2023

suggests a minimum sample size of 20 nests per year and per treatment to estimate nesting success [104]. We then tested whether increasing sampling effort is linked with an increasing proportion of significant effects, using a logistic generalized linear mixed model (GLMM) with R package “lme4” [105], taking study identity as a random factor.

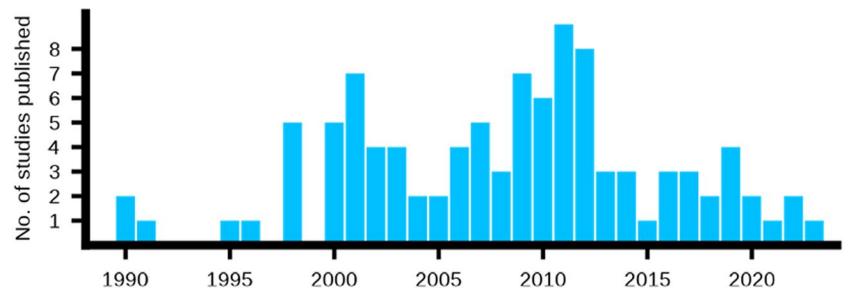
Interpretation of vote-counts may be further complicated by pooling of effects from varying numbers of studies and species subjected to the same MPF intervention, as well as by the varied habitat requirements of those species. Therefore, in order to put study outcomes into context, we extracted information on the species associated with each outcome, namely to which nesting and feeding guild they belong (according to Birds of the World, [106]), and whether they are species of conservation concern, i.e. with a threat status in global [107] or relevant national and subnational red lists (e.g. NatureServe status, for the USA and Canada, [108]). Lastly, we noted down for each study if other variables, such as abundance or clutch size, were measured, as well as any explanations that the authors proposed for the reported breeding success outcomes, especially concerning nest predators and food supply for nestlings. If abundance outcomes were available, we also recorded whether the

direction of MPF effects on species’ abundances matches that of breeding success.

Results

We identified 101 relevant studies (Appendix S1). The search on Web of Science yielded 5339 hits, which were narrowed down to 67 relevant studies after screening (Fig. 1). We then added 4 relevant studies from the Conservation Evidence database and 30 studies resulting from backwards and forwards citation searches (after excluding duplicates). The earliest studies were published in 1990, and since then an average of 3.5 studies were published per year, reaching a maximum of 9 in 2011 (Fig. 2). Studies were published in 31 indexed peer-reviewed journals, besides one study in conference proceedings, one technical report, one doctoral dissertation and one study in a non-indexed journal. Out of the 97 studies, 55 were published in just five journals: Forest Ecology and Management (19 studies), Journal of Wildlife Management (12), Condor/Ornithological Applications (9), Conservation Biology (8) and The Wilson Bulletin/The Wilson Journal of Ornithology (7).

Fig. 2 Publication dates of studies included in this review (last search on 22 November 2023)



Studies were geographically concentrated in North America (Fig. 3), with only 13 studies in Europe, and none found in temperate or boreal regions of Asia, Oceania, Africa or South America. As for the distribution of studies across biomes, nearly half (46 studies) took place in temperate broadleaf & mixed forests, followed by temperate conifer forests (31), and much fewer in boreal forests (5) and Mediterranean forests (5). More than half of the reviewed studies only compared MPF outcomes against an alternative management control (53 studies), whilst 32 studies only used a natural reference control and 16 used both control types. Only 16 studies made use of a before-after control-impact (BACI) study design, and all others but one used a control-impact design. As a whole, 151 bird species are covered (Appendix S2), but nesting or fledging success outcomes are reported at single-species level for only 95 of them, and 57 studies report outcomes for only one species. Among all species covered, there are 118 songbirds from 23 families

(Parulidae being best represented), 17 woodpeckers, 4 hummingbirds, 4 Galliformes, 3 raptors and 5 species from other groups.

We classified the MPF interventions covered by the studies into 11 types (Table 1). The most frequent intervention type was retaining overstorey (37 studies), followed by restoring fire (19) and thinning overstorey (13). Four types were represented by less than five studies: creating dead wood (1), restoring hydrology (2), buffering edges (3) and salvage logging with retention (4). Additionally, MPF types were not represented equally across different biomes (Fig. 4). For instance, studies on the effects of overstorey retention took place mainly in temperate broadleaf and mixed forests, whereas studies on the effects of restoring fire, overstorey thinning and understorey retention took place mainly in temperate conifer forests and temperate conifer savannas. The 101 reviewed studies reported 354 management outcomes, each study reporting between 1

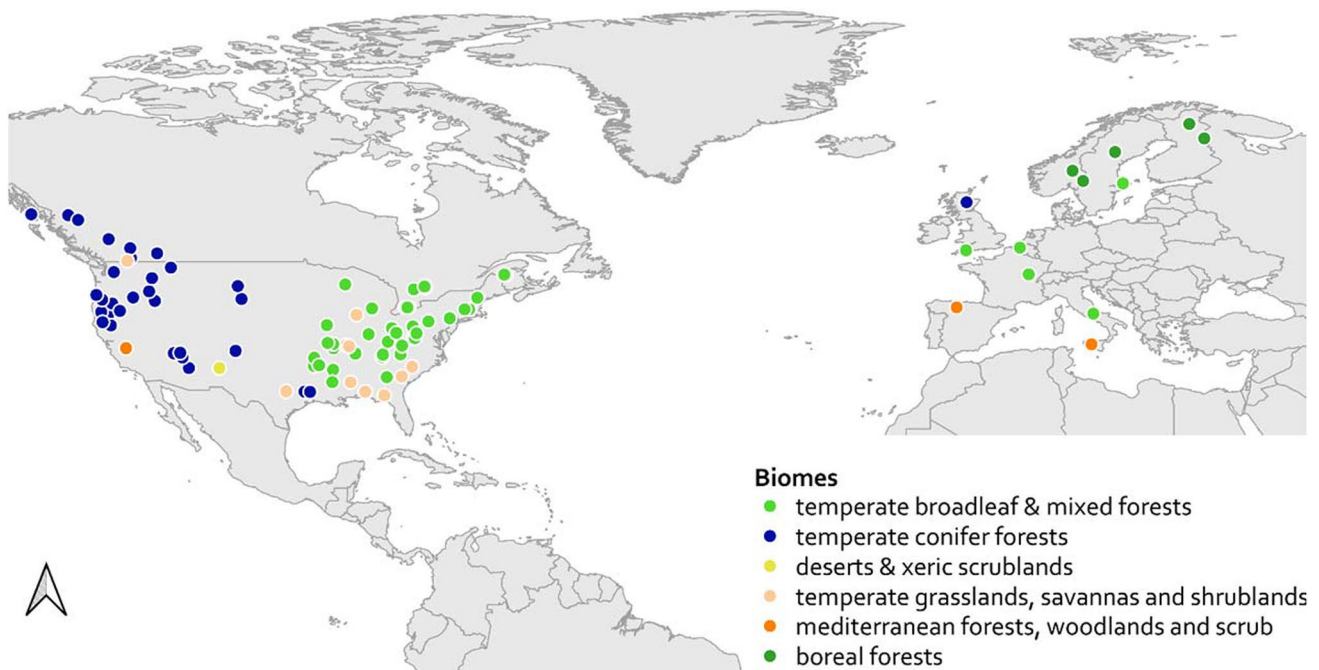
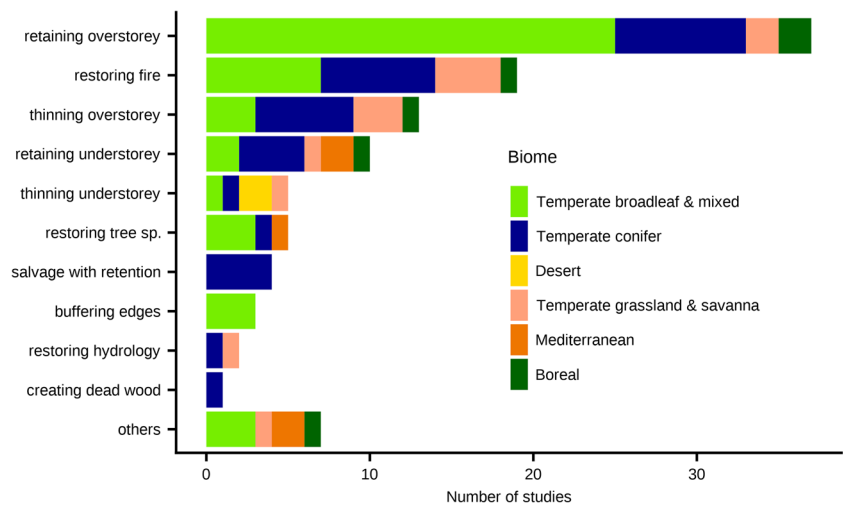


Fig. 3 Geographical distribution of studies included in this review, colour-coded by biome [90]

Fig. 4 Distribution of reviewed studies across 11 MPF types, colour-coded by biome [90]



and 14 outcomes (listed in Appendix S1). Nesting success was much more often reported than fledging success, with 260 and 94 outcomes respectively. The most ubiquitous measure of nesting success was the daily nest survival rate, measured using the Mayfield method [122]. The two species with the highest number of reported outcomes were the great tit (*Parus major*, 14 outcomes) and the wood thrush (*Hylocichla mustelina*, 13 outcomes). The proportion of outcomes found for each nesting guild varied according to the MPF intervention under study, but ground-nesting species were generally underrepresented, especially in regards to overstorey retention (Appendix S3). Sampling effort ranged from 0.2 to 184.8 (median = 10.7) nests per year and per treatment. The proportion of significant outcomes (positive or negative) was not significantly related with sampling effort (logistic GLMM, likelihood ratio test $\chi^2 = 0.6057$, $p = 0.436$, Appendix S4).

When contrasting MPF practices against alternative management practices (AM), the most frequent outcome was a non-significant effect on nesting and fledging success (199 of 239 outcomes, 83%, upper panel of Fig. 5), and for each intervention type individually. This remained true (40 of 49 outcomes) when including only outcomes based on a high sampling effort (> 20 nests monitored per year and sampling unit, Appendix S5). We found 26 positive effects (11%) of MPF on nesting or fledging success when compared with AM, covering seven intervention types, and 14 negative effects (6%), covering six intervention types (upper panel of Fig. 5). Four species of conservation concern—Siberian tit (*Poecile cinctus*), Bachman's sparrow (*Peucaea aestivalis*), white-headed woodpecker (*Leuconotopicus albolarvatus*) and golden-winged warbler (*Vermivora chrysop-tera*)—showed higher breeding success in MPF treatments. Two others—cerulean warbler (*Setophaga cerulea*), prairie warbler (*Setophaga discolor*)—, as well as a group containing hooded warbler (*Setophaga citrina*) and worm-eating

warbler (*Helmitheros vermivorum*), showed instead a lower breeding success in MPF treatments. The full list of species for which positive and negative effects were reported is in Appendix S6. Overstorey retention showed a lower frequency of positive effects (2 of 51) compared with restoring fire (11 of 55). Four intervention types—overstorey retention, understorey retention, edge buffering and restoring hydrology—showed either non-significant or positive effects on breeding success, whereas three intervention types—understorey thinning, dead wood creation and others—showed either non-significant or negative effects. Out of the 239 comparisons with AM controls, 117 were accompanied by abundance data (Appendix S7). In 6 of those instances, concerning 5 species, MPF resulted in both higher breeding success and higher abundance. In 3 cases, concerning 2 species (cerulean warbler and northern cardinal, *Cardinalis cardinalis*), there was indication of an ecological trap, with higher abundance but lower breeding success in MPF treatments. For one species, the wood thrush, MPF (prescribed burning) resulted in lower abundance but higher breeding success, compared to the AM control.

When contrasting MPF practices against natural references (NR), the most frequent outcome was a non-significant effect on nesting and fledging success (84 of 114 outcomes, 74%, lower panel of Fig. 5). This remained true (16 of 22 outcomes) when including only outcomes based on a high sampling effort (Appendix S5). Reported outcomes compared with NR controls were few for most MPF types, except for retaining overstorey, retaining understorey and salvage with retention, and did not exist for three types—buffering edges, restoring hydrology and creating dead wood. Non-significant effects were the most frequent outcome for overstorey retention (57 of 73) and retention in salvage logging (15 of 17), but not for understorey retention. In the case of overstorey retention, a non-significant effect on breeding success was often accompanied by a significant increase in abundance in

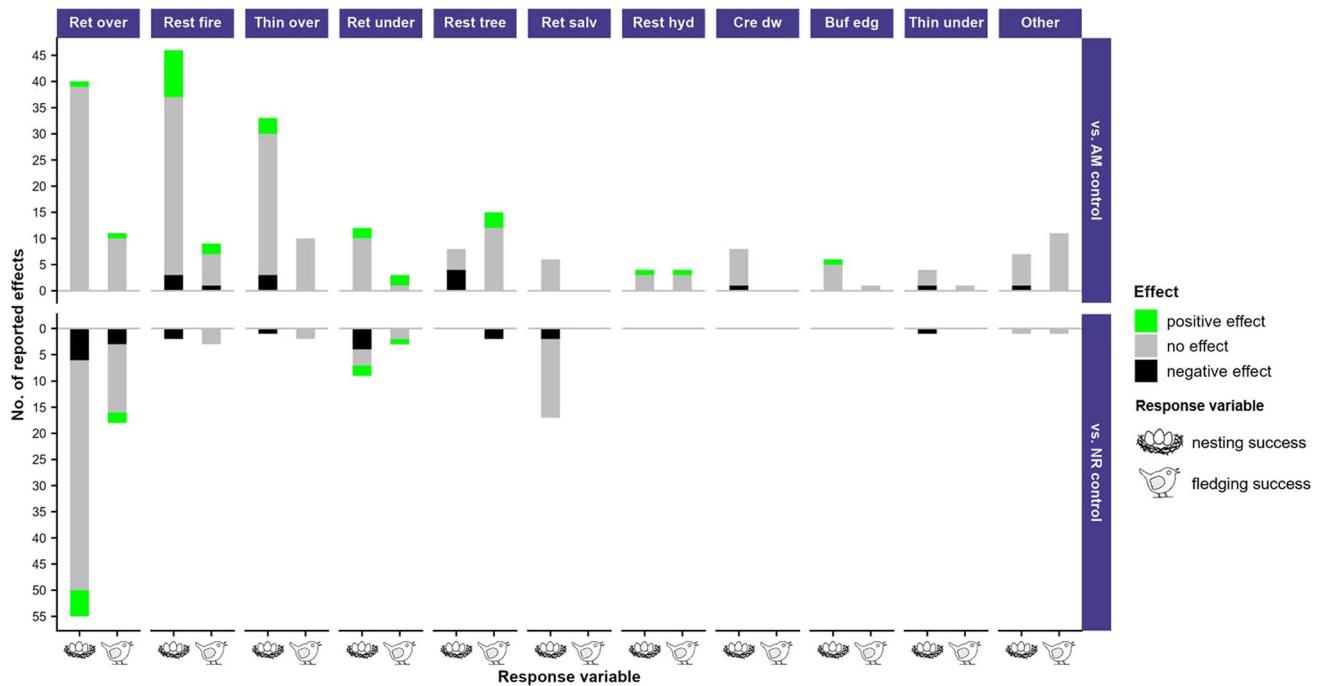


Fig. 5 Number of reported negative, non-significant, and positive outcomes on **nesting success** and **fledging success** (indicated by nest and fledgling icons), when contrasting MPF practices with **alternative management** controls (upper panel) or with **natural reference** controls (lower panel), discriminated by MPF intervention classes (slate-blue labels on top): retaining overstorey (**Ret over**), restoring

fire (**Rest fire**), thinning overstorey (**Thin over**), retaining understorey (**Ret under**), restoring tree species composition (**Rest tree**), salvage with retention (**Ret salv**), restoring hydrology (**Rest hyd**), creating dead wood (**Cre dw**), buffering edges (**Buf edg**), thinning understorey (**Thin under**) and others (**Other**)

MPF treatments, compared to NR controls (20 of 46 instances, Appendix S7). We found 21 negative effects (18%) in comparison to NR, encompassing seven intervention types, and 10 positive effects (9%), covering only two intervention types—overstorey retention and understorey retention. As for species of conservation concern, these were reported to have either lower (8 outcomes) or similar (non-significant, 15 outcomes) breeding success in MPF treatments than in NR controls. The full list of species for which positive and negative effects were reported is in Appendix S6. Three species, two of them of conservation concern—yellow-bellied sapsucker (*Sphyrapicus varius*), olive-sided flycatcher (*Contopus cooperi*) and house wren (*Troglodytes aedon*)—showed evidence of an ecological trap, with decreases in breeding success in MPF treatments concurring with an increase in abundance. Another species, the California towhee (*Melospiza crissalis*) showed the opposite pattern, with higher density in NR controls (long-ungrazed forest) but higher nesting and fledging success in the MPF treatment (a moderately-grazed area).

Discussion

Effects of MPF on Nesting and Fledging Success

Our review indicates that demographic responses of forest bird species to different MPF practices in temperate and boreal forests are mixed and highly context-dependent. We found multiple cases where MPF led to increases in breeding success, several of which referred to species of conservation concern. In contrast, we also identified negative effects and several instances where MPF created ecological traps. Despite that, non-significant effects were the most frequently reported outcome, and this was remarkably consistent across management types, control types and responses analysed. This must be interpreted with caution, due to the small sample sizes of most studies and associated low statistical power. Still, we showed that non-significant effects remained dominant at larger sample

sizes and that positive and negative effects can be of sufficient magnitude to be detected with small sample sizes. Therefore, our results do suggest that stand-level MPF practices frequently lead to neutral or small-magnitude effects on bird breeding success. Given the contribution of low productivity levels to the declining populations of many forest species [112, 123, 124], this highlights a need for complementary management solutions (e.g. [125]) or further adaptation of MPF practices, in order to effectively boost breeding success and fulfil long-term commitments towards forest biodiversity conservation (e.g. [126]).

Studies showing non-significant responses to MPF often identified other factors with a significant influence on nesting and fledging success, pointing the way for management actions that may be more effective at increasing bird productivity. Several studies proposed that retention practices should focus on retaining favoured nesting substrates or high-quality foraging microhabitats for targeted species (e.g. [127–129]), acting on smaller-scale features than usual for MPF. Also for grassland birds, nest survival has been found to be more strongly affected by fine-scale habitat than by patch-level management actions [130]. Other reviewed studies showed that nesting success was rather driven by patterns of nest predation and brood parasitism at larger spatial (e.g. forest fragmentation, in [131]) and temporal scales (e.g. tree masting cycles, in [132]). In landscapes with high forest cover, levels of predation may be low across the landscape (e.g. [133]), and harvest gaps do not provide comparable anthropogenic subsidies to generalist predators [134] and brood parasites [135] as does the proximity to farmland and urbanized areas. Conversely, in highly-fragmented forests, landscapes may be saturated with generalist predators and brood parasites, so that nest success remains overall low, regardless of local management (e.g. [136]). Moreover, in a structurally complex forest environment, where multiple predator guilds are present, MPF may result in compositional turnover of the nest predator assemblage, but not necessarily in overall increases in nest predation [127], as seen for Bachman's sparrows in the context of overstorey thinning [137••]. This possibly explains why prescribed burns lead to lower increases in nest survival in forests than in simpler grassland environments [66]. Manifestly, effects of MPF on nest predation and nesting success are contingent on the identity of prey and predators, and future nest monitoring studies should ascertain nest predator identities, e.g. through camera trapping [138].

When positive effects of MPF on nesting success were found, in comparison with alternative management controls, this was attributed to a change not only in nest predator abundances (e.g. [139, 140]), but also in the accessibility of nests to predators (e.g. [141–143]). For instance, standard thinning practices have been shown to reduce nesting success for boreal forest species

through reduced nest concealment [43, 101], and understorey retention may counteract that effect, an idea which is supported by two of the reviewed studies [142, 143]. Also the restoration of flooding regimes was shown to increase the nesting success of prothonotary warblers (*Protonotaria citrea*), a floodplain forest indicator species, thanks to decreased accessibility of flooded areas to raccoons (*Procyon lotor*), their main nest predator [141]. Furthermore, although none of the reviewed studies investigated this link, MPF may alter the behaviour and habitat selection of nest predators [144], thereby affecting bird nesting success. That is a topic worthy of further investigation, again requiring knowledge of nest predator identities.

Regarding positive effects of MPF on fledging success, several studies on parid species linked that outcome with an improved food supply for nestlings. For the Siberian tit, a specialist of mature forests, overstorey retention was linked to both higher abundances and higher fledging success, in comparison with intensively-managed stands, and this was likely driven by insect availability [145]. Also great tits showed increased feeding activity and fledging success in low-browsing areas in Norway [146]. Both studies are consistent with previous evidence of bottom-up forces driving the abundance and richness of boreal forest songbirds [147, 148]. Fledging success of great tits was also increased where conifer plantations were enriched with broadleaf trees [149], and where exotic or resource-poor native trees were replaced by insect-rich native tree species [150]. Both studies included data on food supply, supporting the assertion that tree species identity is more important than tree diversity in providing food for nestlings. In fact, many foliage-gleaning birds exhibit foraging specialization on less common, early to mid-successional broadleaf tree species with high arthropod densities [151, 152].

As for negative effects of MPF on nesting and fledging success, these were accompanied in several cases by increases in abundance, indicating ecological traps (e.g. [127, 153, 154]). MPF treatments may create such situations due to a combination of attractive foraging conditions with lack of safe nesting sites and high accessibility to brood parasites [127, 155]. Nonetheless, it has been proposed that management measures that consider fine-scale habitat quality (e.g. retaining beech trees with heart rot, for yellow-bellied sapsuckers [127]) can help disarm ecological traps. Negative effects can also arise from the fact that MPF interventions have diverse and sometimes opposing goals (e.g. overstorey retention vs. overstorey thinning or prescribed burns), targeting different species groups, so that any form of MPF risks producing negative impacts on non-targeted species. Among the reviewed studies, the negative effects of prescribed burns concerned primarily ground-nesting species, likely affected by reduction of nest concealment through fire [66]. Fire and fire-surrogate

treatments are known to produce conservation trade-offs for sensitive forest interior species [139, 156, 157] and our results reinforce the need for complementary management strategies at the landscape scale, in order to minimize such trade-offs. Lastly, short-term decreases in breeding success following MPF treatments may not reflect longer-term outcomes. For instance, removal of non-native understorey vegetation can force birds to nest in exposed locations, decreasing nest survival, before native vegetation can fully recover [158], even if native shrubs are ultimately safer nesting sites [159].

Surprisingly, multiple reviewed studies found higher nesting or fledging success in MPF treatments than in natural reference controls (e.g. [128, 160–162]). In the context of understorey retention, this suggests that certain shrub-nesting species, otherwise expected to benefit from a denser understorey, are well-adapted to moderate disturbance of that layer [163]. In the case of overstorey retention, these positive effects reveal that unharvested stands may be inadequate benchmarks, as they carry the legacy of previous management [164], and in such cases birds may actually benefit from small-scale harvests mimicking natural gap formation processes [165].

Implications for Habitat Quality

Even when MPF practices do not affect bird breeding success, that does not necessarily translate into ineffectiveness of MPF in improving habitat quality for birds. In multiple reviewed studies, abundance was measured concurrently with breeding outcomes, and the former increased in response to MPF interventions. There is also an ample body of literature linking various MPF practices with increased abundances of targeted bird species (see [Introduction](#)). This hints that abundance is often limited by factors other than breeding success, and thus abundance can be a suitable indicator for changes in habitat quality with MPF treatments. For instance, no positive effects were reported for salvage with retention, dead wood creation and restoration of traditional Mediterranean silvopastoral systems (in MPF category “others”) on nesting or fledging success, but these interventions primarily targeted cavity-nesting birds, which have high levels of nest survival [63]. Instead, populations of cavity-nesters are limited by the scarcity of suitable nesting sites in production forests [33], an issue which the aforementioned types of MPF help minimizing (see both reviewed studies [121, 166], and others, e.g. [117, 167, 168]). In [169], protecting the understorey from overbrowsing provided more nest sites for orange-crowned warblers, thereby increasing their density (*Leiothlypis celata*), despite no change in nesting success. Birds may also respond to increased food abundance in MPF treatments through denser packing of territories, rather than increased productivity [170, 171], in line with the concept of an ideal free distribution [172].

Moreover, in the case of overstorey retention, although nesting success and abundance may be reduced after harvesting, this form of management remains a preferable alternative to clearcuts, in which nesting habitat for closed-forest specialists is entirely missing [173, 174].

Although we focused on nesting and fledging success, other demographic metrics should not be overlooked when judging the effects of MPF on habitat quality for forest birds. For example, post-fledging survival may be strongly limited by food supply and predation, and limit in turn population growth [175], whilst being also responsive to habitat management [176]. Among our reviewed studies, [177] noted that partial harvests may produce a demographic trade-off for wood thrushes, boosting post-fledging survival even when nesting success is reduced. Also [178] found that burning and overstorey thinning resulted in improved body condition of pied flycatcher (*Ficedula hypoleuca*) nestlings, despite no significant change in fledging success. Food availability can also condition reproductive investment, expressed as number of broods or clutch size [179]. Hence, future demographic studies should incorporate various aspects of the annual cycle of forest birds, to obtain a full picture of their response to MPF interventions.

Research Gaps

In the course of this review, we identified a set of prominent research gaps. Eight MPF types were covered by less than 10 studies each (Table 1), representing priorities for future research. For example, as natural disturbances are on the rise in European forests [180], it is especially relevant to develop salvage logging practices which safeguard biodiversity and forest resilience [181]. Also restoration of hydrological regimes is increasingly applied as a tool to recover boreal forest peatlands (e.g. [182]) and temperate floodplain forests [183], a particularly species-rich habitat [184]. Additionally, the better-studied practices of prescribed burning and overstorey thinning have mostly been evaluated in the context of temperate conifer forests and pine savannas, but fires and other large-scale natural disturbances play an increasingly-recognized role in temperate broadleaf forests [185, 186], thus warranting further research in that biome.

As for the bird species covered, ground-nesters were under-represented in the studies we reviewed. Ground-nesting birds dependent on closed-canopy forests may be particularly sensitive to changes in nest predation driven by harvest gaps and associated change in ground cover [174, 187]. Besides, in our review we noted negative outcomes of prescribed burning for non-targeted ground-nesting birds. Hence, future research on the effects of overstorey retention and prescribed fire should prioritize this bird guild. As for the studied response variables, nesting success was much more often measured than fledging success. High nesting success, as that shown by cavity-nesters

[188], may sometimes not be a good indicator of fledging success. Cavity-nesters show lowered fledging success in salvage-logged areas [189•], but is yet unclear to what degree retention practices could minimize these effects. Studies on fledging success would also be warranted when creating forest edge buffers, given their potential to improve foraging conditions [190].

Studies were patently biased towards temperate North America, a pattern also found in previous systematic reviews on retention forestry practices [32] or on restoration success [191]. This is perhaps the result of the pioneering role of the USA in implementation of MPF practices, such as retention harvests [22] and prescribed burns [109], alongside the establishment of long-term, nation-wide research networks to evaluate these practices, such as the US Forest Service Experimental Forests [192], the Fire and Fire Surrogate Study [193] or the Collaborative Forest Landscape Restoration Program [194]. However, this bias implies that current research is out of step with worldwide implementation of MPF practices, and more demographic studies are needed in other parts of the world. Managed forests cover large swathes of Europe and Asia [195], and increasingly so in boreal regions [9]. MPF practices, under the designation of close-to-nature forestry, and more recently retention forestry, are widely implemented in Europe [196], Japan (e.g. [197]) and in temperate regions of South America [198]. In the fire-prone forests of Australia, the use of prescribed burns is well-established [199] and previous research has examined their effects on bird assemblages (e.g. [200]), but has stopped short of examining demographic responses.

Studies also showed several methodological limitations. Nest-finding is more time-consuming than standard bird surveys, and precise estimates of breeding success require frequent visits (i.e. every 2–4 days) until chicks fledge [56]. Finding nests of certain species may be especially difficult, it may involve disturbance risks for threatened species, and the number of available nests depends on territory density. This implies that breeding success can only be compared between habitats where the species is nesting, and larger nest search areas are needed where densities are lower, so as to ensure sufficient sample size. Moreover, the time and cost of nest monitoring prevent researchers from achieving high sample sizes, that would enable higher statistical power, and from collecting data from multiple independent sites—incurring the risk of pseudoreplication, and thus limiting reliability and reproducibility of findings. One option to ensure sufficient sample sizes is to aggregate nest data within bird functional groups (e.g. nesting guild), as done in several reviewed studies. That approach, however, obscures intra-guild variation across species in their responses to management [201]. Another promising alternative is to use reproductive activity indices (e.g. [202]), as implemented in two studies we reviewed [203, 204], or even behavioural observations alongside point count surveys [205]. Still, caution

is needed with these approaches, due to low detectability of relevant behaviours in forest habitats [206], and local validation with nest monitoring data is still recommended.

Adaptive management provides unique opportunities for demographic studies, as research can take advantage of large extents of forests undergoing management changes [71, 92••]. Nonetheless, adaptive management studies still suffer from short durations [207], and only a few of the studies we reviewed covered more than 10 years after intervention. Only longer-term monitoring can assess the effect of retaining structures across harvesting rotations, or detect time-lagged responses of nest predators. Studies covering large spatial and temporal scales would also facilitate the use of BACI experimental designs—which were uncommon in the reviewed studies but provide the best-quality evidence [86]—and improve the chance of finding adequate natural references (as in [178]). Indeed, more than half of the studies did not include natural references as controls, and especially for prescribed burns and overstorey thinning, control stands under natural disturbance regimes (e.g. [208]) are lacking.

Conclusions and Management Implications

The studies we reviewed reveal that, whilst stand-level MPF practices appear to have limited effects on the nesting and fledging success of boreal and temperate forest birds, this may be attributed to a mismatch between the scale of management and the scale at which ecological processes act, especially nest predation. Other tools, such as landscape-level planning (e.g. [209]), predator control [66], and fine-scale provision of specific microhabitats (e.g. [127, 210]) should complement MPF in order to boost productivity for species of conservation interest. MPF practices can still contribute to improve habitat quality for birds in managed forests, but abundance and other demographic metrics are potentially better-suited indicators of habitat quality at that scale than nesting or fledging success. Nonetheless, for particular species and intervention types, including species of conservation concern, we found evidence of positive breeding success outcomes. With this review, we offer an annotated list of studies from which practitioners may glean valuable information for their specific management scenarios. Moreover, several biomes, intervention types and species groups were underrepresented in the reviewed studies. The lack of context-specific research is a recognized obstacle for the implementation of conservation measures by practitioners [211]. Thus, we also call for continued development of locally-relevant studies on the effects of MPF on bird demographics, focusing on the set of research gaps we identified.

There is still insufficient evidence as to how MPF practices could be combined and upscaled, given the varying benefits of different MPF types for different sets of species, possible

trade-offs for non-targeted species, and the economic costs associated with long-term application of management prescriptions. Furthermore, management decisions are strongly driven by the intuitive knowledge of practitioners [211], which may condition which practices they are willing to implement, i.e. the “knowing-doing gap”, and ultimately which practices are studied. Researchers themselves are in a unique position to develop innovative management approaches [212], testing the boundaries of current management traditions (e.g. [28]). Therefore, we argue for the need of ecosystem-wide experimental studies, focused on species of conservation concern, where management actions are tested across spatial scales, and which combine abundance measures, demographics and functional links with nest predators and food resources (see [213•]), if possible also quantifying the associated economic costs (see [35]). The advancement of sustainable forest management depends on both innovative experimental approaches and context-specific studies on current practices, so MPF can fully deliver on its conservation promises.

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Data Availability Reviewed studies and their details are listed in the Supplementary Information.

Declarations

Competing interests The authors declare no competing interests.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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