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Habitat restoration benefits wild bees: a meta-analysis

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ABSTRACT

1. Pollinator conservation is of increasing interest in light of managed honeybee (*Apis mellifera*) declines, and declines in some species of wild bees. Much work has gone into understanding the effects of habitat enhancements in agricultural systems on wild bee abundance, richness, and pollination services. However, the effects of ecological restoration targeting "natural" ecological endpoints (e.g., restoring former agricultural fields to historic vegetation types or improving degraded natural lands) on wild bees have received relatively little attention, despite their potential importance for countering habitat loss.
2. We conducted a meta-analysis to evaluate the effects of ecological restoration on wild bee abundance and richness, focusing on unmanaged bee communities in lands restored and managed to increase habitat availability and quality. Specifically, we assessed bee abundance and/or richness across studies comparing restored vs. unrestored treatments and studies investigating effects of specific habitat restoration techniques, such as burning, grazing, invasive plant removal and seeding.
3. We analysed 28 studies that met our selection criteria: these represented 11 habitat types and 7 restoration techniques. Nearly all restorations associated with these studies were performed without explicit consideration of habitat needs for bees or other pollinators. The majority of restorations targeted plant community goals, which could potentially have ancillary benefits for bees.
4. Restoration had overall positive effects on wild bee abundance and richness across multiple habitat types. Specific restoration actions, tested independently, also tended to have positive effects on wild bee richness and abundance.
5. *Synthesis and applications.* We found strong evidence that ecological restoration advances wild bee conservation. This is important given that habitat loss is recognized as a leading factor in pollinator decline. Pollinator responses to land management are rarely evaluated in non-agricultural settings and so support for wild bees may be an underappreciated benefit of botanically focused management. Future restoration projects that explicitly consider the

needs of wild bees could be more effective at providing nesting, foraging and other habitat resources. We encourage land managers to design and evaluate restoration projects with the habitat needs of wild bee species in mind.

Keywords

Abundance, bees, burning, conservation, grazing, habitat, land management, pollinators, restoration, species richness

Introduction

Bees are arguably the most important pollinators worldwide (Buchmann and Nabhan 1996), responsible for the majority of pollination in agricultural and natural systems (National Research Council 2007). Recent declines in bee species, and their importance as ecosystem service providers, have brought bees to the forefront of conservation efforts. For bee species with documented losses and in geographic regions with historic bee community data available, habitat loss is a frequently cited factor in bee declines (Grixti et al. 2009, Winfree et al. 2009, Cameron et al. 2011). To combat habitat loss, there has been considerable research evaluating the effectiveness of habitat enhancements for wild bees in otherwise developed landscapes, such as agricultural systems or cities (Shepherd et al. 2003, Vaughan 2008, Grixti et al. 2009, Pawelek et al. 2009, Dicks et al. 2010, MacIvor and Packer 2015, Hall et al. 2016).

To date, most bee conservation efforts have focused on providing resources for wild bees (e.g., nesting and foraging resources) within otherwise human-dominated land uses (Shepherd et al. 2003, Batáry et al. 2010). In a recent meta-analysis, habitat enhancements for wild bees were found to be effective in agricultural systems (Scheper et al. 2013). For example, addition of native hedgerows or planting of wildflowers in field margins can provide consistent foraging opportunities, leading to greater wild bee diversity and abundance (Pywell et al. 2005, Haaland et al. 2011, Pywell et al. 2012). Likewise, installing nesting boxes or maintaining patches of bare, untilled ground have been found to provide nesting habitat (Wesserling and Tscharntke 1995, Severns 2004, Dicks et al. 2010). In residential and urban areas, similar habitat enhancements can provide nesting and foraging resources for wild bees (Shepherd et al. 2003, but see MacIvor and Packer 2015). These enhancements have led to greater bee abundance and diversity relative to unmanipulated control sites in city parks and residential neighbourhoods (Frankie et al. 2009, Hernandez et al. 2009, Pawelek et al. 2009), yet the extent to which habitat enhancements provide resources for a functionally diverse suite of wild bees remains uncertain (Woodcock et al. 2014a).

On a larger scale, ecological restoration of undeveloped lands (e.g., degraded natural areas or restoration of former working lands, such as agricultural fields, back to pre-settlement habitats) of may be an effective conservation tool to counter the effects of habitat loss on wild bees. Through restoration, practitioners assist the recovery of an ecosystem that has been degraded, damaged or destroyed (SER 2004). Historically, habitat restoration has focused on plant community outcomes, and restoration management techniques frequently involve direct manipulation of the plant community (Young 2000). Typical restoration actions include removal of invasive plant species, seeding and planting of native flora, reinstating historic fire regimes, reintroducing grazers, and other regionally habitat-specific management actions.

Theoretically, restoration could be a ‘tide that raises all ships,’ improving habitat quality by directly altering plant communities. For example, vegetation dominated by a single invasive plant species provides little diversity in floral resources or bloom times, limiting the portfolio of bees that can be supported (M’Gonigle et al. 2016). In such cases, increased plant diversity associated with invasive species management and subsequent restoration of a desirable botanical community could increase foraging opportunities for bees. These actions could lead to increases in bee abundance and richness, similar to habitat augmentations in agricultural areas (Scheper et al. 2013). Unlike small-scale enhancements of otherwise developed sites, restoration of natural areas can also return larger areas of contiguous habitat for native bees, returning landscape-level and metacommunity processes (Montoya et al. 2012).

However, there is also potential for actions associated with restoration to act as disturbances to wild bees (Moretti et al. 2009, Williams et al. 2010). For example, removal of invasive species and burning or mowing without immediate replacement of mature plants may reduce foraging opportunities available to bees. Prescribed burning is commonly used in restoration to alter habitat structure and clear invasive or undesired vegetation; early in a restoration project, fire frequency may exceed that of the historic burn cycle (Packard 1997). While burning could reveal more bare ground for soil nesters through removal of herbaceous litter, burning also removes standing dead material, such as the pithy stems and dead wood that many species require for nests (Michener 2000). Burning and other disturbances are likely to differentially affect bees representing different nesting guilds, or even those of similar guilds found across different habitats (Moretti et al. 2009).

We conducted a meta-analysis to evaluate the overall impact of habitat restoration on wild bees, and the relative impact of specific management techniques (i.e., burning, grazing, overall restoration, ecological compensation meadows, invasive plant removal, mowing and seeding). Through meta-analysis we could calculate the relative and overall effect sizes of each restoration action and for restoration overall, while incorporating study size and replication into the strength of each response. We considered wild bee richness and/or abundance as responses and restricted our analysis to restorations targeting "natural" end-points, e.g., grasslands or forests, but not anthropogenic or novel habitats like farms, housing developments or urban gardens. We retained studies of ecological compensation meadows, which are large-scale (i.e., multiple hectare) efforts to convert land used for hay production or pasturing to closer approximations of wild habitats. While these lands have an agricultural component, we considered them more comparable to grassland restorations than to crop production systems; as livestock grazing is a recognized tool for restoring grasslands in both Europe and North America (Hayes and Holl 2003, Dostálek and Frantík 2008).

We hypothesized that (1) habitat restoration would have generally positive effects on wild bee abundance and richness, (2) overall restoration would have a greater positive impact on wild bee abundance or richness than any one restoration action tested independently and (3) some specific restoration actions would function as disturbances, with negative effects on bee abundance or richness.

Materials and Methods

Literature search

To identify relevant studies we searched Web of Science (Clarviate Analytics 2015) using the following term combinations "bee AND (restor* OR habitat manag* OR habitat enhanc*)" with topic filters of "ecology" and "biodiversity conservation" on December 6, 2016. This search yielded 412 papers.

From this point, we individually examined studies and excluded those that took place within production agricultural settings (e.g., pollinator-friendly hedgerows around tomato fields) or focused on managed bees such as honeybees (*Apis mellifera*). We included studies that evaluated the effects of restoration overall (e.g., restored vs. unrestored comparisons) and studies of specific management actions frequently implemented in restoration (e.g., mowing, grazing and burning) that took place in degraded lands and former agricultural lands that were converted to pre-settlement conditions. We did not evaluate the effects of habitat remediation in lands that had been structurally transformed and/or polluted by human activities (e.g., strip mines, landfills, or quarries). After identifying a total of 38 papers that met our criteria, we searched within the references in these papers for additional suitable studies. This yielded an additional 9 papers, for a total of 47.

Calculation of effect sizes

Of the 47 studies, 28 contained data suitable for analysis, i.e., bee abundance and/or species richness were reported before and after restoration treatments or compared between restored vs. unrestored treatments in the article itself, in supplemental information, or in communications with the authors (see Table S1 in Supporting Information). For the 19 excluded studies, data were not reported in a way that allowed us to calculate bee richness or abundance (e.g., authors reported total number of insects and insect species) and raw data were either unavailable or did not provide the necessary information (e.g., only insect counts were reported, not bees specifically). From the final 28 studies, we extracted a total of 70 data points for inclusion in the meta-analyses. For studies with multiple categorical treatments, we extracted multiple data points comparing each test variable (e.g., low-intensity grazing and high-intensity grazing) to the control or reference condition, as described in Koricheva et al. (2013). For 14 papers, both wild bee abundance and richness were reported as response variables to restoration or management actions.

We calculated Hedge's *d*, an unbiased standardized mean difference corrected for small sample size, which is suitable for meta-analyses with few studies (Hedges and Olkin 1985, Koricheva et al. 2013). The effect size *d* can be interpreted here as the inverse-variance-weighted difference in abundance or richness of bees between restored and unrestored or reference conditions, measured in units of standard deviation. Large effect sizes can result from a large difference in mean bee abundance or diversity between treatments or from a small estimate of the pooled variance between treatments.

Whenever possible, we calculated effect size based on reported sample size, mean and standard deviation values of bee abundance or richness for each treatment (Koricheva et al. 2013). If data were not available, we emailed the corresponding author requesting these data. For studies where the author did not respond or necessary data were not available, we calculated an effect size based on a reported *F*-test or using mean and standard deviation values extracted from figures using Web Plot Digitizer (Rohatgi 2015). For studies with a continuous design (e.g., bee response to grazing intensity), we ran a Fischer's *z* transformation on the correlation coefficient *r* to calculate an effect size and then converted this value to Hedge's *d* using the metafor package (Viechtbauer 2010) in R version 3.3.3 (R Development Core Team 2015).

In our calculations of Hedge's *d* we were not able to account for variance arising from measurement error in the underlying studies. Measurement error could arise from factors such as misidentification of specimens, differences in identification skill or data-entry errors. As articles included in this meta-analysis did not report measurement errors, we were unable to perform study-level corrections or attempt to calculate an average error correction term. That said, ecologists do increasingly attempt to estimate measurement error, as reviewed by Morrison (2016), and its incorporation into ecological meta-analyses may become more common – as is the case, for example, in medical research (Schmidt and Hunter 2015).

Analyses of effect size and heterogeneity

All statistical analyses were performed in R version 3.3.3 (R Development Core Team 2015) using the package metaphor (Viechtbauer 2010). For each response variable (bee abundance or richness), we created a random effects model with study and restoration action (burning, grazing, overall restoration, ecological compensation meadows, invasive plant removal, mowing and seeding) as random factors to account for non-independence between different treatments within the same study or of responses to the same treatment across studies. Models were fitted using restricted maximum-likelihood estimation (Koricheva et al. 2013).

We grouped studies by restoration action (Table 1) and constructed models within each of these categories with study as a random factor to account for non-independence. To determine if effect sizes across studies were similar, we calculated heterogeneity (*Q*) within each restoration category and for all studies combined.

Publication bias and sensitivity analyses

To explore the possibility of publication bias we constructed funnel plots – scatter plots of effect sizes against a measure of their variance – to determine if reported studies were unbalanced, as recommended by Koricheva et al. (2013). A publication bias toward significant results would create an asymmetrical funnel, typically missing small studies with non-significant effects. Having found funnel asymmetry, we used trim-and-fill plots to estimate "missing" studies. We then updated mean effect sizes with imputed missing studies, and compared original and updated mean effect sizes using *t*-tests. Finally, we calculated Rosenberg's weighted fail-safe number (Rosenberg 2005), an estimate of the number of unpublished studies with an effect size of zero that would need to be added to make the observed effect size non-significant ($p > 0.05$).

Results

Overall, restoration in general and specific restoration actions had positive effects on bee abundance ($d = 1.49$, 95% CI = 0.92, 2.06, $p < 0.0001$, Fig. 1) and richness ($d = 1.01$, 95% CI = 0.65, 1.38, $p < 0.0001$, Fig. 2). Effects of restoration and management differed by study and were heterogeneous for bee abundance ($Q = 637.50$, d.f. = 38, $p < 0.0001$, Figure 1) and richness ($Q = 117.88$, d.f. = 31, $p < 0.0001$, Fig. 2).

Of the 70 data points identified, 39 reported wild bee abundance and 31 reported wild bee richness (see Table S1). The majority of studies were conducted in Europe (n = 17) and North America (n = 10 United States, n = 1 Canada) with 2 additional studies conducted, at least partially, in Israel. These included studies that evaluated the effects of restoration in general and creation of ecological compensation meadows, as well as mowing, burning, grazing, invasive plant removal and seeding (Table S1).

Mean effect sizes of restoration and heterogeneity among studies: Bee abundance

All restoration categories had positive mean effect sizes for bee abundance (Fig. 1). The greatest effect size was attributed to a removal and mulching treatment of the invasive plant Chinese privet (*Ligustrum sinense*) in a woodland (Hanula and Horn 2011). Invasive plant removal had the greatest positive effect on bee abundance ($d = 4.84$, 95% CI = 3.59, 6.09, $p < 0.0001$, Fig. 1). Negative effects of restoration on bee abundance were found in two mowing studies and one grazing study (Fig. 1). Bee abundance outcomes were significantly heterogeneous within mowing and grazing categories, respectively (Q = 500.41, d.f. = 4, $p < 0.0001$ and Q = 29.32, d.f. = 12, $p < 0.003$, Table 1); other restoration actions did not exhibit significant heterogeneity between individual study results (Table 1).

Mean effect sizes of restoration and heterogeneity among studies: Bee richness

With the exception of mowing, all restoration actions had significant positive effects on bee richness (Fig. 2). Invasive plant removal had the greatest positive effect on richness (d = 6.38, 95% CI = 2.55, 10.20, p = 0.001, Fig. 2), though studies within this category were heterogeneous with respect to their individual effect sizes (Q = 32.81, d.f. = 4, $p < 0.0001$, Table 1). Two individual studies found negative effects on bee richness; Russel et al. (2005) reported a negative effect of continuous mowing of powerline strips relative to unmown controls, and Potts et al. (2006) found fewer species of bees in pine forests that had been burned for 10 or more years compared to unburned controls. Grazing, ecological compensation meadows, and invasive plant removal groups were all heterogeneous in effect sizes (Q = 11.29, d.f. = 4, $p < 0.02$; Q = 19.02, d.f. = 3, $p < 0.001$; Q = 32.81, d.f. = 4, $p < 0.0001$, respectively Table 1); other restoration actions did not exhibit significant heterogeneity.

Evidence of publication bias

Asymmetrical funnel plots indicated potential publication bias, specifically that studies with low effect sizes and high standard errors (located in the lower left quadrant) were “missing”. Trim and fill analysis estimated zero missing studies for abundance (SI Fig. 1a), but four missing studies for richness (SI Fig. 1b). Inclusion of these missing studies would slightly decrease effect-size estimates but still maintain a significant positive effect of restoration on bee richness (d = 0.84, 95% CI [0.31, 1.37], p = 0.002).

Calculation of Rosenberg’s fail-safe number indicated that 1,299 studies with null results for effects of restoration on bee richness would be needed to make the observed effect non-significant ($p > 0.05$); 3,103 such studies would be needed to make the effect of restoration on bee abundance non-significant. These results provide robust evidence of significant, positive effects of restoration on wild bee abundance and species richness.

Discussion

Overall, ecological restoration had a positive effect on wild bee abundance and richness across multiple studies, habitat types, and geographic regions. With the exception of mowing, all restoration categories had net positive effects on bee abundance and bee richness (Figs. 1 & 2). The effects of restoration on bee abundance and richness ranged from nearly 10-fold increases (Fielder et al. 2012) to non-significant effects; no restoration categories were found to have negative mean effects (*d*).

Of the 28 studies evaluated in this meta-analysis, only 5 stated that bee habitat support and conservation were explicit goals of restoration efforts. Restorations tend to be completed with plant community outcomes in mind (Young 2000), with reference plant communities in high-quality remnant sites as ideal targets. Bees and other pollinators have frequently fallen under the "Field of Dreams" hypothesis: "if we build it, they will come" (Hilderbrand 2005), as opposed to having habitats explicitly designed and managed for their needs. If restorations are producing positive effects on wild bee abundance and richness without explicit consideration of their habitat needs, perhaps incorporating bee considerations into restoration planning and design could further increase the benefits provided to bees by ecological restoration, as has been demonstrated in enhanced agricultural systems (Scheper et al. 2013).

Restoration or management techniques could be directly or indirectly affecting bee abundance or richness. For example, grazing and burning commonly employed in grassland restoration can stimulate floral blooming (Packard 1997), leading to more potential foraging sites for bees. However, techniques such as burning could also directly impact bee abundance and richness via the physical disturbance itself, e.g., by destroying overwintering larvae in stem or twig nests. Overall, as most of the restoration techniques evaluated in this meta-analysis were focused on plant-community outcomes, the indirect benefits of a "higher-quality" plant community are the most likely drivers of patterns in bee abundance and richness.

Identifying gaps and future research opportunities

Over 90% of the studies that fit our selection criteria were performed in North America or Europe, which also means the restoration techniques examined here may not be representative of global restoration efforts. Studies tended to be from grasslands (e.g., prairie and savanna) and forests, on lands that had been heavily impacted by invasive plant species, were former agricultural fields, or were being used as "working" grasslands for grazing or hay production. As demonstrated by Moretti et al. (2009), the response of bees to restoration actions cannot be assumed to be the same across habitat types or regions. Though a strength of a meta-analytical approach is to synthesize effect sizes across studies, this approach is sensitive to the size and diversity of the pool of available studies. Further research addressing bee responses to restoration in more parts of the world, in more habitat types, and with respect to more management actions is needed to gain a deeper understanding of the benefits of restoration to bees.

It is important to note that data on community composition of bees were not available for most studies, thus we were unable to perform analyses of how different types of bees responded to restoration (e.g., cavity-dwelling vs. soil-dwelling bees). For example, evidence from agricultural systems suggests habitat enhancements promote increased functional redundancy in bee communities (Woodcock et al. 2014a). Williams et al. (2010) found that bees' responses to disturbance were mediated by their traits, and Tonietto et al. (2017) found that bee functional trait composition varied among restorations of different age. As species lists are more commonly published and archived, functional analysis of wild bee species' responses to restoration will become possible.

Conservation implications and recommendations for management

Habitat restoration can help to counteract habitat loss, the greatest threat to wild bee abundance and richness (Winfree et al. 2009). Here, we document an overall positive effect of habitat restoration on wild bee abundance and richness, even when restoration planning and goalsetting did not explicitly consider the habitat needs of wild bees. This is important, considering a recent survey found that only 11% of grassland managers in the Midwestern USA considered the habitat needs of wild bees during the restoration process (Harmon-Threatt and Chin 2016).

To better support wild pollinators, recent studies have documented the importance of designing restoration seed mixes for forbs with overlapping bloom times and multiple floral morphologies (Harmon-Threatt and Hendrix 2014, Havens and Vitt 2016, M'Gonigle et al. 2016). For many localities, pollinator friendly plant species lists have already been developed (e.g., Mader 2010) for use in managed lands or residential gardens. Our findings raise the possibility that still greater conservation results for bees could be achieved were land managers to take the additional step of incorporating bee foraging and nesting needs as design considerations (e.g., Shepherd 2002, Shepherd et al. 2003, Shepherd et al. 2008, Vaughan 2008).

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Authors' contributions

R.K.T. and D.J.L. conceived the study. R.K.T. collected and analysed data and drafted the article. R.K.T. and D.J.L. revised the article and gave final approval for publication.

Data accessibility

All data used in this manuscript are present in the manuscript and its supporting information, and are available from the Dryad Digital Repository. DOI: http://dx.doi.org/10.5061/dryad.q1791 (Tonietto and Larkin, 2017)

Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1. Studies included in analyses. Includes measures of Hedge's *d* and variance, response and test variables and full citations.

Figure S1. Trim-and-fill funnel plots indicating publication bias for studies reporting effects of restoration on a) wild bee abundance and b) wild bee richness. Filled circles represent publications included in the meta-analysis; open circles are "missing" studies estimated by imputation. The vertical line represents the mean effect size updated to include the estimated influence of missing and real studies.

Table 1. Heterogeneity of effect sizes (Q) between studies within restoration categories for the response variables wild bee abundance and species richness.

	Abundance			Richness		
Restoration category	d.f.	*Q*	*p*	d.f.	*Q*	*p*
Restoration	4	3.87	0.42	4	4.89	0.28
Ecological compensation meadows				3	19.02	0.0003
Burning	6	10.98	0.08	6	8.26	0.21
Grazing	12	29.32	0.003	4	11.29	0.02
Invasive plant removal	4	2.89	0.57	4	32.81	<0.0001
Mowing	5	537.78	<0.0001	3	7.19	0.06
Seeding	2	1.94	0.37			

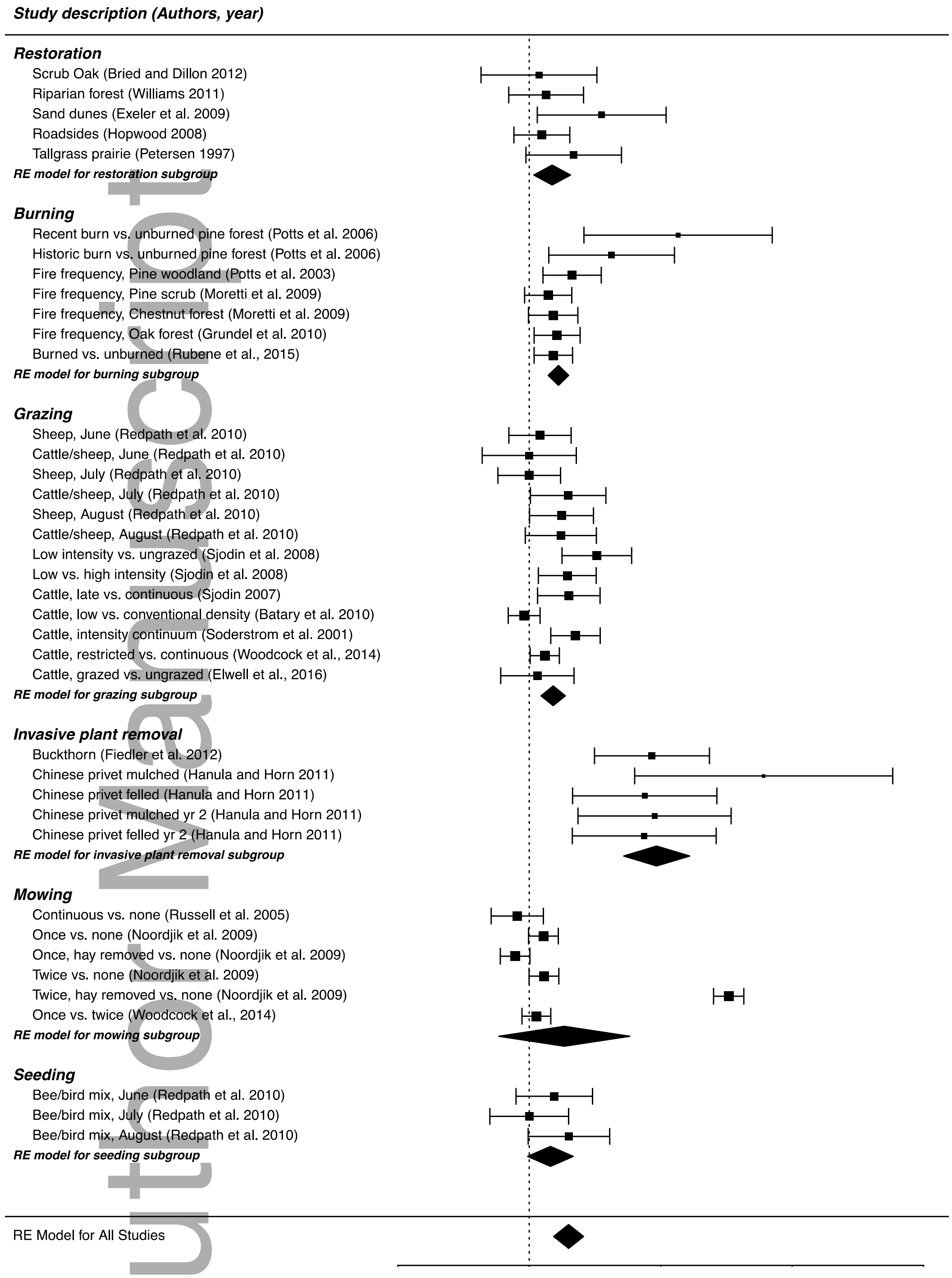

Figure 1 The effects of habitat restoration on wild bee abundance. Forest plot showing effect size (Hedge's *d*) and 95% C.I. calculated for each study. The diamond below each category represents the mean effect size for all studies within the group based on a random effects model. The random effects model encompassing all studies from all subgroups is reported at the bottom

of the forest plot. The dotted line represents an effect size of zero.

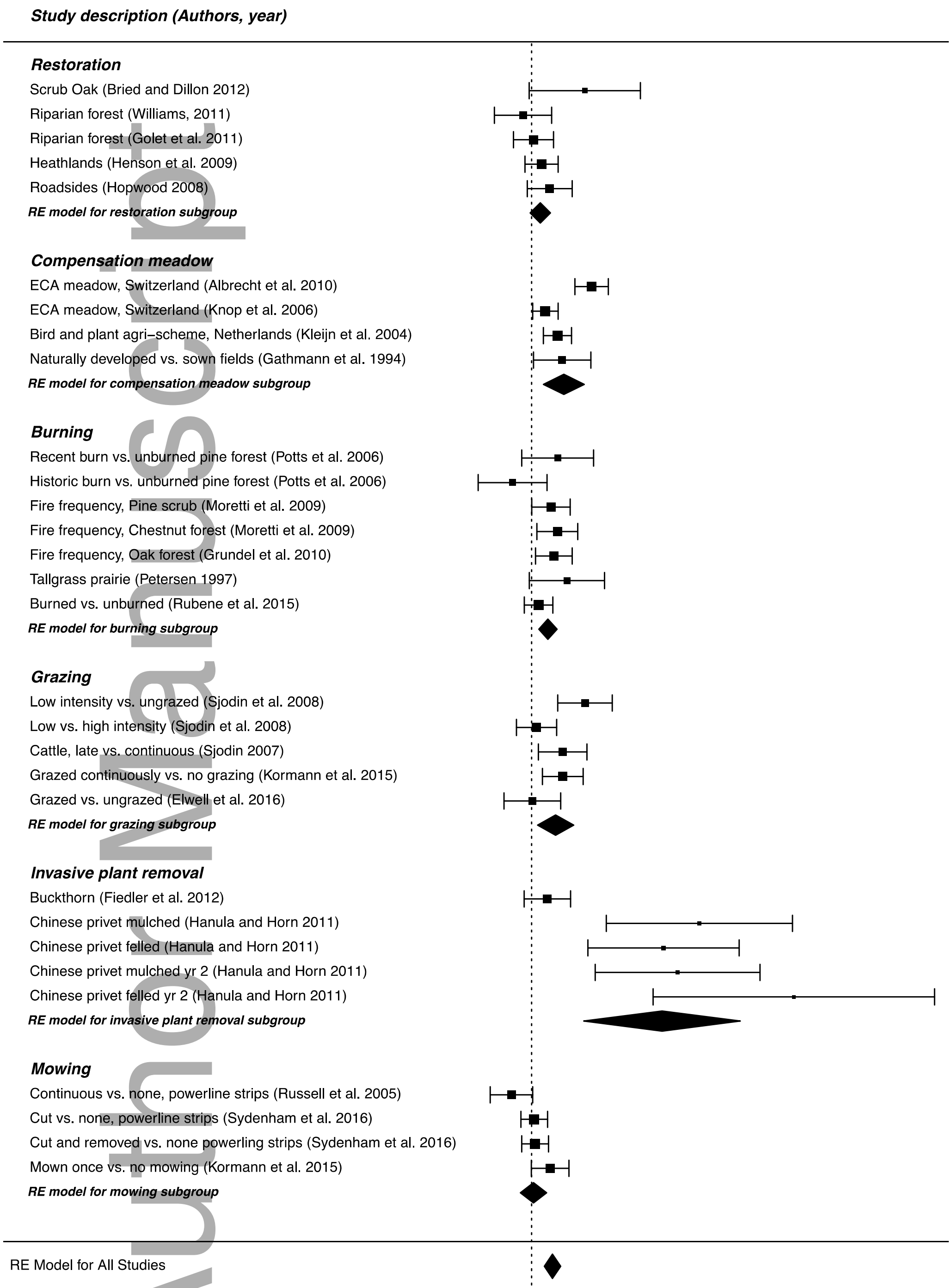

Figure 2 The effects of habitat restoration on wild bee richness. Forest plot showing effect size (Hedge's *d*) and 95% C.I. calculated for each study. The diamond below each category represents the mean effect size for all studies within the group based on a random effects model.

The random effects model encompassing all studies from all subgroups is reported at the bottom of the forest plot. The dotted line represents an effect size of zero.

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