ECOLOGY LETTERS

Ecology Letters, (2013) doi: 10.1111/ele.12082

LETTER

A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems

Christina M. Kennedy,[1*†] Eric Lonsdorf,[1] Maile C. Neel,[2] Neal M. Williams,[3] Taylor H. Ricketts,[4] Rachael Winfree,[5] Riccardo Bommarco,[6] Claire Brittain,[3,7] Alana L. Burley,[8] Daniel Cariveau,[5] Luísa G. Carvalheiro,[9,10,11] Natacha P. Chacoff,[12] Saul A. Cunningham,[13] Bryan N. Danforth,[14] Jan-Hendrik Dudenhöffer,[15] Elizabeth Elle,[16] Hannah R. Gaines,[17] Lucas A. Garibaldi,[18] Claudio Gratton,[17] Andrea Holzschuh,[15,19] Rufus Isaacs,[20] Steven K. Javorek,[21] Shalene Jha,[22] Alexandra M. Klein,[7] Kristin Krewenka,[15] Yael Mandelik,[23] Margaret M. Mayfield,[8] Lora Morandin,[18] Lisa A. Neame,[16] Mark Otieno,[24] Mia Park,[14] Simon G. Potts,[24] Maj Rundlöf,[6,25] Agustin Saez,[26] Ingolf Steffan-Dewenter,[19] Hisatomo Taki,[27] Blandina Felipe Viana,[28] Catrin Westphal,[15] Julianna K. Wilson,[20] Sarah S. Greenleaf[29] and Claire Kremen[29]

Abstract

Bees provide essential pollination services that are potentially affected both by local farm management and the surrounding landscape. To better understand these different factors, we modelled the relative effects of landscape composition (nesting and floral resources within foraging distances), landscape configuration (patch shape, interpatch connectivity and habitat aggregation) and farm management (organic vs. conventional and local-scale field diversity), and their interactions, on wild bee abundance and richness for 39 crop systems globally. Bee abundance and richness were higher in diversified and organic fields and in landscapes comprising more high-quality habitats; bee richness on conventional fields with low diversity benefited most from high-quality surrounding land cover. Landscape configuration effects were weak. Bee responses varied slightly by biome. Our synthesis reveals that pollinator persistence will depend on both the maintenance of high-quality habitats around farms and on local management practices that may offset impacts of intensive monoculture agriculture.

Keywords

Agri-environment schemes, diversified farming system, ecologically scaled landscape index, ecosystem services, farm management, habitat fragmentation, landscape structure, organic farming, pollinators.

Ecology Letters (2013)

[1] *Urban Wildlife Institute, Lincoln Park Zoo, Chicago, IL, 60614, USA*
[2] *Department Plant Science and Landscape Architecture, University of Maryland, College Park, Maryland, 20742, USA*
[3] *Department of Entomology, University of California, One Shields Ave., Davis, CA, 95616, USA*
[4] *Gund Institute for Ecological Economics, University of Vermont, Burlington, VT, 05401, USA*
[5] *Department of Entomology, Rutgers University, New Brunswick, NJ, 08901, USA*
[6] *Department of Ecology, Swedish University of Agricultural Sciences, SE-75007, Uppsala, Sweden*
[7] *Section Ecosystem Functions, Institute of Ecology, Leuphana University of Lüneburg, Scharnhorststraße 1, 21335, Lüneburg, Germany*
[8] *School of Biological Sciences, The University of Queensland, Goddard Building, St Lucia Campus, Brisbane, QLD, 4072, Australia*
[9] *Institute of Integrative and Comparative Biology, University of Leeds, Leeds, LS2 9JT, UK*
[10] *NCB-Naturalis, postbus 9517, 2300 RA, Leiden, The Netherlands*
[11] *Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa*
[12] *Instituto de Ecología Regional (IER), Facultad de Ciencias Naturales e IML, UNT. CC 34, 4107, Tucumán, Argentina*
[13] *CSIRO Ecosystem Sciences, GPO Box 1700, Canberra, ACT 2601, Australia*
[14] *Department of Entomology, Cornell University, Ithaca, NY, 14853, USA*
[15] *Department of Crop Sciences, Agroecology, Georg August University Göttingen, Grisebachstr, 6 D-37077, Göttingen, Germany*
[16] *Department of Biological Sciences, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada*
[17] *Department of Entomology, University of Wisconsin, 1630 Linden Drive, Madison, WI, 53706, USA*
[18] *Sede Andina, Universidad Nacional de Río Negro (UNRN) and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Mitre 630, CP 8400, San Carlos de Bariloche, Río Negro, Argentina*
[19] *Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am Hubland, 97074, Würzburg, Germany*
[20] *Department of Entomology, Michigan State University, East Lansing, MI, 48824, USA*
[21] *Agriculture and Agri-Food Canada, Atlantic Food and Horticultural Research Centre, 32 Main Street, Kentville, NS, B4N 1J5, Canada*
[22] *Integrative Biology, 401 Biological Laboratories, University of Texas, Austin, TX, 78712, USA*
[23] *Department of Entomology, The Hebrew University of Jerusalem, P.O. Box 12, Rehovot, 76100, Israel*
[24] *School of Agriculture, Policy and Development, University of Reading, Reading, RG6 6AR, UK*
[25] *Department of Biology, Lund University, SE-223 62, Lund, Sweden*
[26] *Laboratorio Ecotono-CRUB, Universidad Nacional del Comahue - INIBIOMA, (8400) San Carlos de Bariloche, Río Negro, Argentina*
[27] *Department of Forest Entomology, Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki, 305-8687, Japan*
[28] *Biology Institute, Federal University of Bahia – UFBA, Rua Barão de Geremoabo, s/n Campus Universitário de Ondina, Salvador, BA, 40170-210, Brazil*
[29] *Department of Environmental Science, Policy and Management, University of California, Berkeley, CA, 94720-3114, USA*
[†] *Current affiliation:Development by Design Program, The Nature Conservancy, Fort Collins, CO, 80524, USA*
**Correspondence: E-mail: ckennedy@tnc.org*

INTRODUCTION

Wild bees are a critical component of ecosystems and provide essential pollination services to wild plants (Kearns *et al.* 1998) and to crops (Klein *et al.* 2007) in agricultural landscapes. In some situations, wild bees alone can fully pollinate crops (Kremen *et al.* 2002; Winfree *et al.* 2007b), and bee richness can enhance the magnitude and temporal stability of pollination (Kremen *et al.* 2002; Klein *et al.* 2009; Garibaldi *et al.* 2011). However, growers often rely on the managed honey bee (*Apis mellifera*) to provide crop pollination. *Apis* declines in regions of the United States and Europe (Potts *et al.* 2010b), concomitant with increases in pollination-dependent crop cultivation globally, have increased the potential for pollination shortfalls for farmers (Aizen *et al.* 2008). These factors in turn increase the importance of wild pollinators (Potts *et al.* 2010b). It is therefore vital to determine the environmental conditions, both at local and landscape scales, that support diverse and abundant wild bee assemblages in agroecosystems.

Two drivers are proposed to influence wild bee abundance and richness on farms: local management practices on the farm and the quality and structure of the surrounding landscape (Kremen *et al.* 2007). There is growing evidence for the importance of local field management on wild pollinators, both separately and in interaction with landscape effects, as revealed in regional studies (Williams & Kremen 2007; Rundlöf *et al.* 2008; Batary *et al.* 2011; Concepción *et al.* 2012). Different management practices, such as organic farming or increasing within-field habitat heterogeneity, can improve bee abundance, richness and productivity even in landscapes with little natural habitat (Williams & Kremen 2007; Holzschuh *et al.* 2008; Rundlöf *et al.* 2008; Batary *et al.* 2011), as long as sufficient habitat exists to maintain source populations (Tscharntke *et al.* 2005, 2012). Whether these local-scale and interactive effects are consistent across global agriculture remains unknown.

Research on landscape-level effects on pollinators has focused predominantly on the contribution of natural and semi-natural areas surrounding farms, which may provide essential habitats and key floral resources and nesting sites that contribute to the long-term persistence of wild bees (Westrich 1996; Williams & Kremen 2007). Syntheses of data across multiple taxa, crop species and biomes reveal that bee visitation, richness and stability increase with decreasing distance from these habitats (Ricketts *et al.* 2008; Garibaldi *et al.* 2011). These studies offer insights into the importance of natural areas in sustaining pollination services in human-modified landscapes, but their use of binary landscape categories (e.g. natural and semi-natural habitat vs. cropland) fails to account for the complexity of different habitats known to provide partial resources for bees (Westrich 1996; Winfree *et al.* 2007a). These recent syntheses also do not consider species' responses to local-scale management practices or differential responses to habitat attributes.

To develop a more robust understanding of how different land-cover types influence wild (bee) pollinators in agricultural landscapes, a spatially explicit model has been developed to predict relative bee abundance based on the composition of habitats and their floral and nesting resources (Lonsdorf *et al.* 2009). The Lonsdorf *et al.* (2009) model produces an ecologically scaled landscape index (*sensu* Vos *et al.* 2001) that captures the estimated quality and amounts (and potential seasonal shifts) of habitats in a landscape, and is scaled based on species mobility. This model, however, does not account for variation caused by different farm management practices; and it does not account explicitly for landscape configuration (i.e. the spatial arrangement of habitat patches in a landscape), which can impact floral, nesting and overwintering resources for bees (Kremen *et al.* 2007) and has been hypothesised to be an important, yet unaccounted for determinant of bee communities (Lonsdorf *et al.* 2009).

Here, we performed an empirical synthesis to disentangle the independent and interactive effects of local management and landscape structure on wild bees, which is essential to inform ecosystem service-based land use recommendations in agroecosystems (Tscharntke *et al.* 2005, 2012). We apply the Lonsdorf *et al.* (2009) model to 39 studies on 23 crops in 14 countries on 6 continents to capture landscape composition effects on bee richness and abundance, accounting for the floral and nesting value of all habitat types in a landscape. We expand on previous analyses by determining the influence of landscape configuration (patch shape, interpatch connectivity and habitat aggregation) and local farm management (organic vs. conventional farming and local-scale field diversity). Using mixed model analysis in a model selection framework, we then test the relative importance of landscape composition (i.e. model output), landscape configuration, local farm management and their potential interactions, as predictors of observed wild bee abundance and richness in crop fields.

METHODS

Studies and measures of pollinators

We analysed pollinator and landscape data from 605 field sites from 39 studies in different biomes (tropical and subtropical, $n = 10$; Mediterranean, $n = 8$; and other temperate, $n = 21$) and on 23 crops with varying degrees of dependency on pollinators (Table 1, see Appendix S1 for references of published studies and Appendix S2 for methods of unpublished studies in Supporting Information). Our analyses focused on bees because they are considered the most important crop pollinators (Klein *et al.* 2007) and their biology is relatively well known. We analysed only wild species, because the abundance of managed species depends more on human choice of placement than on landscape or local field site characteristics. We targeted studies that sampled bees at multiple independent fields within an agricultural landscape (across a gradient in agricultural intensity) based on author knowledge and previous synthetic work (Ricketts *et al.* 2008; Garibaldi *et al.* 2011). Author(s) of each study provided site-specific data on (1) bee abundance and/or visitation and bee richness, (2) spatial locations of fields, (3) characterisation of local management (organic vs. conventional and field diversity), (4) GIS data on surrounding multi-class land cover and (5) estimates of nesting and floral resource quality for different bee guilds for each land-cover class. Within studies, all sites were separated by distances of 350 m–160 km (mean ± SD: 25 ± 22 km), with only 0.02% site pairs located < 1 km apart (Appendix S3).

Bee abundance and richness

All 39 studies measured bee abundance on ($n = 22$) or number of visits to ($n = 17$) crop flowers, and all but one study measured species richness (Table 1). Abundance was quantified as the number of individual bees collected from aerial netting, pan trapping or both; bee visitation was measured as the total number of times a bee

Table 1 Studies included in the modelling of local and landscape effects on global wild bee assemblages

Study	Citation[§]	Crop species	Crop pollinator dependence*	Bee flower visitors modelled	Honey bee: managed, feral[$]	# Years sampled	# Sites	Site distance range (mean) (m)	Location
Tropical and subtropical biomes[†]									
Coffee_A	Jha & Vandermeer 2010	*Coffea arabica*	Medium (10–40%)	44 taxa: *Augochlora* spp., *Augochlorella* sp., *Augochloropsis* spp., *Caenaugochlora* sp., *Ceratina* spp., *Dialictus* spp., *Euglossa* sp., *Halictus* spp., *Melitoma* spp., *Melissodes* sp., *Plebia* sp., *Trigona* sp., *Trigonisca* sp., *Xylocopa* sp.	Yes, yes	1	7	>925–4030 (2470)	Chiapas, Mexico
Coffee_B	Ricketts 2004; Ricketts *et al.* 2004	*C. arabica*	Medium (10–40%)	11 taxa: *Apis* sp., *Melipona* sp., *Nannotrigona* sp., *Partamona* sp., *Plebeia* sp., *Plebia* sp., *Trigona* spp., *Trigonisca* sp.	No, yes	1	8	>490–3100 (1400)	San Isidro del General, Costa Rica
Grapefruit	Chacoff & Aizen 2006; Chacoff *et al.* 2008	*Citrus paradisi*	Little (< 10%)	14 taxa: *Apis mellifera*, *Augochlorospis* spp., *Bombus* sp., *Dialictus* sp., *Megachilidae* sp., *Plebeia* spp., *Psaenythia* sp., *Tetragonisca* sp., *Trigona* spp.	No, yes	3	12	>430–74 000 (33 200)	Yungas, Argentina
Longan	Blanche *et al.* 2006	*Dimocarpus longan*	Medium (10–40%)	3 taxa: *A. mellifera*, *Homalictus dampieri*, *Trigona carbonaria*	No, yes	1	6	>2500–80 000 (43 000)	Queensland, Australia
Macadamia_A	Blanche *et al.* 2006	*Macadamia integrifolia*	Essential (>90%)	1 taxon: *A. mellifera*	No, yes	1	5	>10 000–40 000 (24 000)	Queensland, Australia
Macadamia_B	Mayfield (unpublished data)	*Macadamia integrifolia*	Essential (>90%)	1 taxon: *Trigona carbonaria*	Yes, yes	1	10	>430–24 000 (13 300)	New South Wales, Australia
Mango	Carvalheiro *et al.* 2010	*Mangifera indica*	High (40–90%)	3 taxa: *Ceratina* spp., *Xylocopa* sp.	Yes, yes	1	12	>1700–13 600 (6500)	Limpopo, South Africa
Passion flower	Viana & Silva (unpublished data)	*Passiflora edulis Sims f. flavicarpa*	Essential (>90%)	4 taxa: *A. mellifera*, *Trigona spinipes*, *Xylocopa (Megaxylocopa) frontalis*, *Xylocopa (Neoxylocopa) grisescens*	No, yes	1	16	>1000–9600 (4400)	Bahia, Brazil
Pigeon pea	Otieno *et al.* (unpublished data)	*Cajanus cajan*	Little (< 10%)	48 taxa: *Amegilla* spp., *Anthidium* sp., *Anthophora* sp., *Braunsapis* sp., *Ceratina* sp., *Coelioxys* sp., *Dactylurina* sp., *Euaspis* sp., *Halictus* sp., *Heriades* sp., *Hypotrigona* sp., *Lasioglossum* sp., *Lipotriches* sp., *Lithurge* sp., *Macrogalea* sp., *Megachile* spp., *Meliponula* sp., *Melissodes* sp., *Nomia* sp., *Pachyanthidium* sp., *Pachymelus* sp., *Plebeina* sp., *Pseudapis* sp., *Pseudoanthidium* sp., *Pseudophilanthus* sp., *Systropha* sp., *Tetralonia* sp., *Tetraloniella* sp., *Thyreus* sp., *Xylocopa* spp.	Yes, no	1	12	>2100–35 000 (16 300)	Kibwezi District, Kenya

(continued)

Table 1. (continued)

Study	Citation[§]	Crop species	Crop pollinator dependence*	Bee flower visitors modelled	Honey bee: managed, feral[$]	# Years sampled	# Sites	Site distance range (mean) (m)	Location
Sunflower_A	Carvalheiro *et al.* 2011	*Helianthus annuus*	Medium (10–40%)	4 taxa: *Lasioglossum* sp., *Megachile* sp., *Tetraloniella* sp., *Xylocopa* sp.	Yes, yes	1	30	>350–24 000 (8400 m)	Limpopo, South Africa
Mediterranean biome									
Almond_A	Klein *et al.* 2012; Klein, Brittain, & Kremen (unpublished data)	*Prunus dulcis*	High (40–90%)	38 taxa: *Agapostemon* sp., *Andrena* spp., *Bombus* sp., *Ceratina* spp., *Eucera* spp., *Habropoda* sp., *Halictus* spp.; *Hoplitis* sp., *Lasioglossum* spp., *Micralictoides* sp., *Osmia* spp., *Panurginus* sp., *Protosmia* sp., *Stelis* sp.	Yes, no	1	23	>1460–46 000 (17 600)	California, USA
Almond_B	Kremen (unpublished data)	*P. dulcis*	High (40–90%)	8 taxa: *Andrena* sp., *Bombus* sp., *Dialictus* sp., *Halictus* spp., *Lasioglossum* sp.	Yes, no	1	15	>1150–54 100 (25 400)	California, USA
Almond_C	Mandelik (unpublished data) (a)	*P. dulcis*	High (40–90%)	27 taxa: *Andrena* spp., *Ceratina* spp., *Eucera* spp., *Halictus* sp., *Lasioglossum* spp., *Nomada* spp.	Yes, no	1	6	>1100–23 000 (13 100)	Judean Foothills, Israel
Sunflower_B	Greenleaf & Kremen 2006 (b)	*H. annuus*	Medium (10–40%)	13 taxa: *Agapostemon* sp., *Anthophoridae* spp., *Bombus* spp., *Halictus* spp., *Lasioglossum* sp., *Megachile* spp., *Svastra* sp., *Xylocopa* sp.	Yes, no	3[¶]	15	1400–55 000 (20 600)	California, USA
Sunflower_C	Mandelik (unpublished data) (b)	*H. annuus*	Medium (10–40%)	60 taxa: *Andrena* spp., *Ceratina* spp., *Ceylalictus* sp., *Colletes* sp., *Eucera* spp., *Halictus* spp., *Hylaeus* spp., *Lasioglossum* spp., *Nomada* spp., *Nomioides* sp., *Osmia* sp., *Panurgus* sp., *Systropha* sp.	Yes, no	1	13	1200–26 600 (11 050)	Judean Foothills, Israel
Tomato_A	Greenleaf & Kremen 2006 (a)	*Solanum lycopersicum*	Little (< 10%)	4 taxa: *Anthophora urbana*, *Bombus vosnesenskii*, *Lasioglossum incompletus*, Small striped bee	Yes, no	1	10	2900–58 000 (27 100)	California, USA
Watermelon_A	Kremen *et al.* 2002, 2004	*Citrullus lanatus*	Essential (>90%)	17 taxa: *Agapostemon* sp., *Anthophora* sp., *Bombus* spp., *Calliopsis* sp., *Halictus* spp., *Hylaeus* sp., *Lasioglossum* spp., *Melissodes* spp., *Osmia* sp., *Peponapis* sp., *Sphecodes* sp., *Triepeolus* sp.	Yes, no	2[¶]	34	>410–69 500 (25 240)	California, USA
Watermelon_B	Mandelik (unpublished data) (c)	*C. lanatus*	Essential (>90%)	47 taxa: *Ceratina* spp., *Ceylalictus* sp., *Eucera* spp., *Halictus* spp., *Hylaeus* spp., Lasioglossum spp., *Lithurgus* sp., *Megachile* spp., *Nomada* spp., *Nomiapis* spp., *Ochreriades* sp., *Xylocopa* sp.	Yes, no	1	19	>935–30 100 (14 000)	Judean Foothills, Israel

(continued)

Table 1. (continued)

Study	Citation[§]	Crop species	Crop pollinator dependence*	Bee flower visitors modelled	Honey bee: managed, feral[$]	# Years sampled	# Sites	Site distance range (mean) (m)	Location
Other temperate biomes[‡]									
Apple	Park & Danforth (unpublished data)	*Malus domestica*	Essential (>90%)	58 taxa: *Andrena* spp., *Augochlora* sp., *Augochlorella* sp., *Augochloropsis* sp., *Bombus* spp., *Ceratina* sp., *Colletes* sp., *Halictus* spp., *Lasioglossum* spp., *Nomada* spp., *Osmia* spp., *Sphecodes* sp., *Xylocopa* sp.	Yes, yes	2[¶]	14	>2500–110 000 (52 200)	New York, USA
Blueberry_A	Isaacs & Kirk 2010	*Vaccinium corymbosum, cv. Jersey*	High (40–90%)	4 taxa: *Andrena* spp., *Bombus* spp., *Halictidae* spp., *Xylocopa* sp.	Yes, no	1	12	>1200–10 200 (36 000)	Michigan, USA
Blueberry_B	Javorek (unpublished data)	*Vaccinium angustifolium*	Essential (>90%)	18 taxa: *Andrena* spp., *Augochlorella* sp., *Bombus* spp., *Colletes* sp., *Halictus* spp., *Lasioglossum* spp., *Osmia* spp.	Yes, no	3	16	>2000–155 700 (66 000)	Prince Edward Island, Canada
Blueberry_C	Tuell *et al.* 2009	*Vaccinium corymbosum*	High (40–90%)	101 taxa: *Agapostemon* spp., *Andrena* spp., *Augochlora* sp., *Augochlorella* sp., *Augochloropsis* sp., *Bombus* spp., *Ceratina* spp., *Colletes* spp., *Halictus* spp., *Hoplitis* spp., *Hylaeus* spp., *Lasioglossum* spp., *Megachile* spp., *Nomada* spp., *Osmia* spp., *Sphecodes* spp., *Xylocopa* sp.	Yes, no	3	15	>2800–80 400 (31 600)	Michigan, USA
Buckwheat	Taki *et al.* 2010	*Fagopyrum esculentum*	High (40–90%)	17 taxa: *Apis cerana*, *Chalicodoma* sp., *Coelioxys* sp., *Colletes* spp., *Epeolus* sp., *Halictus* sp., *Hylaeus* spp., *Lasioglossum* spp., *Lipotriches* sp., *Megachile* spp., *Sphecodes* sp., *Xylocopa* sp.	Yes, no	2	17	450–9500 (3500)	Ibaraki, Japan
Canola_A**	Arthur *et al.* 2010	*Brassica napus and juncea*	Medium (10–40%)	2 taxa: *A. mellifera*, native bees	No, yes	1	19	>375–27 497 (11 100)	Boorowa New South Wales, Australia
Canola_B	Prache, MacFadyen, & Cunningham (unpublished data)	*B. napus and juncea*	Medium (10–40%)	12 taxa: *Amegilla* sp., *Lasioglossum* spp., *Leioproctus* spp., *Lipotriches* sp.	Yes, yes	1	10	>530–6400 (4100)	Bethungra New South Wales, Australia
Canola_C	Bommarco, Marini & Vaissière 2012	*Brassica napus*	Medium (10–40%)	8 taxa: *Bombus* spp.	Yes, no	1	10	>3850–71 000 (26 700)	Uppland, Sweden
Canola_D	Morandin & Winston 2005	*Brassica rapa and napus*	High (40–90%)	86 taxa: *Andrena* spp., *Anthidium* sp., *Anthophora* spp., *Bombus* spp., *Coelioxys* spp., *Colletes* spp., *Diadasia* sp., *Eucera* sp., *Halictus* spp., *Heriades* sp., *Hoplitis* spp., *Hylaeus* spp., *Lasioglossum* spp., *Megachile* spp., *Melissodes* sp., *Nomada* spp., *Osmia* spp., *Panurginus* sp., *Protandrena* spp., *Sphecodes* spp., *Stelis* sp.	No, no	2*	54	>480–67 700 (24 600)	Alberta, Canada

(continued)

Table 1. (continued)

Study	Citation[§]	Crop species	Crop pollinator dependence*	Bee flower visitors modelled	Honey bee: managed, feral[$]	# Years sampled	# Sites	Site distance range (mean) (m)	Location
Cantaloupe	Winfree *et al.* 2008	*Cucumis melo*	Essential (>90%)	18 taxa: *Agapostemon* sp., *Andrena* sp., *Augochlora* sp., *Augochlorella* sp., *Bombus* spp., *Ceratina* sp., *Halictus* spp., *Lasioglossum* sp., *Megachile* sp., *Melissodes* sp., *Peponapis* sp., *Triepeolus* sp., *Xylocopa* sp.	Yes, no	1	14	>2200–72 300 (35 000)	New Jersey & Pennsylvania, USA
Cherry	Holzschuh, Dudenhöffer, & Tscharntke 2012	*Prunus avium*	High (40–90%)	25 taxa: *Andrena* spp., *Bombus* spp., *Lasioglossum* spp., *Nomada* sp., *Osmia* sp.	Yes, no	1	8	>900−7600 (4000)	Hesse, Germany
Cranberry_A	Cariveau (unpublished data)	*Vaccinium macrocarpon*	High (40–90%)	43 taxa: *Andrena* spp., *Augochlora* sp., *Augochlorella* sp., *Augochloropsis* spp., *Bombus* spp., *Ceratina* sp., *Coelioxys* spp., *Heriades* sp., *Hoplitis* sp., *Hylaeus* sp., *Lasioglossum* spp., *Megachile* spp., *Melitta* sp., *Nomada* spp., *Osmia* spp., *Panurginus* sp., *Sphecodes* sp., *Xylocopa* sp.	Yes, no	1	16	>1000–33 000 (15 700)	New Jersey, USA
Cranberry_B	Gaines (unpublished data)	*V. macrocarpon*	High (40–90%)	106 taxa: *Agapostemon* spp., *Andrena* spp., *Augochlora* sp., *Augochlorella* sp., *Bombus* spp., *Calliopsis* sp., *Ceratina* spp., *Coelioxys* sp., *Colletes* sp., *Halictus* spp., *Hoplitis* spp., *Hylaeus* spp., *Lasioglossum* spp., *Macropis* sp., *Megachile* spp. *Melissodes* sp., *Nomada* sp., *Osmia* spp., *Sphecodes* spp., *Stelis* sp.	Yes, no	1	15	>3200–56 000 (27 000)	Wisconsin, USA
Field bean	Carré *et al.* 2009	*Vicia faba*	Little (< 10%)	44 taxa: *Andrena* spp., *Bombus* spp., *Coelioxys* sp., *Halictus* sp., *Lasioglossum* spp., *Nomada* spp., *Sphecodes* sp.	Yes, no	1	10	3700–39 000 (23 900)	South East England
Pepper	Winfree *et al.* 2008	*Capsicum annuum*	Little (< 10%)	15 taxa: *Augochlora* sp., *Augochlorella* sp., *Bombus* spp., *Halictus* sp., *Lasioglossum* spp.	Yes, no	1	21	>1100–72 200 (34 700)	New Jersey & Pennsylvania, USA
Red clover	Bommarco *et al.* 2012; Rundlöf & Bommarco (unpublished data)	*Trifolium pratense*	Essential (>90%)	15 taxa: *Bombus* spp.	Yes, no	2[¶]	25	>860–119 000 (54 600)	Skane, Sweden
Squash	Neame & Elle (unpublished data)	*Curcurbita pepo, C. moschata, C. maxima*	Essential (>90%)	24 taxa: *Agapostemon* spp., *Bombus* spp., *Ceratina* spp., *Dialictus* sp., *Halictus* spp., *Lasioglossum* spp., *Melissodes* spp.	Yes, no	1	9	>420–26 500 (9960)	Okanagan-Similkameen Valley, BC, Canada
Strawberry	Carré *et al.* 2009; Steffan-Dewenter, Krewenka, Vaissière & Westphal (unpublished data)	*Fragaria sp.*	Medium (10–40%)	28 taxa: *Andrena* spp., *Bombus* spp., *Halictus* spp., *Lasioglossum* spp., *Nomada* spp., *Osmia* spp., *Sphecodes* sp.	Yes, no	1	10	>3870–49 300 (24 000)	Lower Saxony, Germany

(continued)

Table 1. (continued)

Study	Citation[§]	Crop species	Crop pollinator dependence*	Bee flower visitors modelled	Honey bee: managed, feral[$]	# Years sampled	# Sites	Site distance range (mean) (m)	Location
Sunflower_D	Sáez, Sabatino, & Aizen 2012	*H. annuus*	Medium (10–40%)	9 taxa: *Augochlora* sp., *Augochloropsis* sp., *Bombus* sp., *Dialictus* sp., *Halictus* spp., *Megachile* sp., *Melissoptila* sp., *Xylocopa* sp.	Yes, yes	1	21	>370–68 100 (22 900)	SE Pampas, Argentina
Tomato_B	Winfree *et al.* 2008	*S. lycopersicum*	Little (< 10%)	16 taxa: *Andrena* sp., *Augochlora* sp., *Augochlorella* sp., *Augochloropsis* sp., *Bombus* spp., *Halictus* sp., *Lasioglossum* spp.	Yes, no	1	13	>1500–89 100 (39 000)	New Jersey & Pennsylvania, USA
Watermelon_C	Winfree *et al.* 2007b	*C. lanatus*	Essential (>90%)	46 taxa: *Agapostemon* spp., *Augochlora* sp., *Augochlorella* sp., *Augochloropsis* sp., *Bombus* spp., *Calliopsis* sp., *Ceratina* spp., *Halictus* spp., *Hylaeus* spp., *Lasioglossum* spp., *Megachile* spp., *Melissodes* sp., *Peponapis* sp., *Ptilothrix* sp., *Triepeolus* sp., *Xylocopa* sp.	Yes, no	1	23	>875–89 500 (36 800)	New Jersey & Pennsylvania, USA

*Dependence of crops on pollinators for reproduction based on Klein *et al.* (2007): low dependence (< 10% yield reduction without pollinators), modest (10–40%), high (40–90%) or essential (>90%).

†Studies located in tropical (< 23.5° latitude in both hemispheres) and subtropical zones (between 20° and 40° latitude in both hemispheres), collectively referred to as tropical.

‡Studies located at >23.5° and < 66.5° north latitude, except those with Mediterranean climate (warm to hot, dry summers and mild to cold, wet winters).

[$] *A. mellifera* modelled when only feral and non-managed: Canola_A, Coffee_B, Grapefruit, Longan, Macadamia_A and Passion flower studies.

¶Majority of sites only sampled in 1 year.

**Richness not modelled because native bee species not resolved taxonomically.

[§] See Appendix S1 for complete references for published studies; and Appendix S2 for methodology of unpublished studies.

landed on, foraged from or touched a flower per plot or transect in a given time interval (hereafter collectively referred to as abundance). When studies measured both visits and abundance, we used the latter estimate, which provided the finest taxonomic resolution. In almost 75% of cases, richness was to species-level (n = 502 of 675 taxa), but sometimes it was based on morphospecies (n = 6), species-group (n = 15), subgenera (n = 34), genera (n = 113), genus-group (n = 3) or body size classes (n = 2) (*sensu* Michener 2000). As social bees may be more sensitive than solitary bees to habitat isolation (Ricketts *et al.* 2008) and human disturbance (Williams *et al.* 2010), we characterised each species as social or solitary. Social species included highly eusocial (e.g. *Melipona*, *Trigona*, *Apis*) to primitively eusocial or semi-social species (e.g. most bumble bees and many Halictinae such as *Lasioglossum* and *Halictus*) (Michener 2000).

Local and landscape variables

For each study, we obtained (1) a characterisation of two aspects of local farm management (organic vs. conventional farming and local-scale field diversity), (2) an ecologically scaled measure of landscape composition using the Lonsdorf *et al.* (2009) model and (3) statistical measures of landscape configuration using the program FRAGSTATS 3.3 (McGarigal *et al.* 2002).

Local farm management

To characterise farm management, fields were categorised by authors as organic (i.e. lacking or having highly reduced use of herbicides, fertilisers and pesticides, n = 91) or conventional (i.e. primarily using synthetic inputs to cultivate crops, n = 514), and as locally diverse (fields < 4 ha, with mixed crop types within or across fields and/or presence of non-crop vegetation, such as hedgerows, flower strips, and/or weedy margins or agroforestry, n = 173) or locally simple (monocultural fields $\geq$ 4 ha, lacking crop or other plant diversity, n = 432). Field type and field diversity were not necessarily coupled, with 38% of fields being organic and locally simple, whereas 21% of fields were conventional and locally diverse; therefore, we examined the independent and potentially interactive effects of these two management variables.

Landscape composition

We characterised landscape composition around farm sites using the Lonsdorf *et al.* (2009) model, which produces an ecologically scaled index of habitat quality in a two-step process. First, using the GIS land cover it calculates pollinator 'supply' at each pixel (30 m × 30 m cell), based on the suitability of the surrounding land cover for nesting and floral resources, assuming that nearby resources contribute more than distant resources (based on an exponential function parameterised by the typical species' foraging distance). Second, using the pollinator supply values, the model predicts an expected abundance of pollinators arriving at any given pixel, again assuming that pollinator supply from nearby pixels contributes more than that from pixels farther away. The model produces a quality index (0–1) of total pollinator abundance at any site in the landscape, which we refer to as the 'Lonsdorf landscape index' (LLI) (see Appendix S4 for further detail).

We calculated the LLI for field sites within the 39 study regions. Authors assigned nesting and floral suitability values to land-cover classes, and overall floral values were calculated as a weighted sum across seasons (permitting coding of temporal variation in floral resources). Highest overall habitat suitabilities (aggregated across nesting and floral resources) were assigned to natural and semi-natural areas (i.e. shrubland, grassland, forest and woody wetlands) and to a lesser extent certain croplands (i.e. orchards and vineyards, pasture and fallow fields and perennial crops) and low density development and open spaces (Table S4_2). Authors also coded each bee species or group by nesting guild and designated their flight period. For all expert-derived parameters (i.e. floral and nesting values, nesting guild and seasonality), authors consulted independent data sources when available. We generated LLI for each bee species, and then aggregated into total abundance over all bee species by weighting indices by study-wide relative abundances of corresponding species. The Lonsdorf model was implemented using ArcGIS, and is available through the Natural Capital Project ('Crop Pollination' tool within the InVEST Software, http://www.naturalcapitalproject.org/InVEST.html) (Tallis *et al.* 2011).

Landscape configuration

We quantified habitat configuration 3 km around field sites using landscape-level metrics in the program FRAGSTATS 3.3 (McGarigal *et al.* 2002), to coincide with the spatial extent of the Lonsdorf model and typical foraging ranges of bees (Greenleaf *et al.* 2007) (Figure S5_1). We examined metrics that captured aspects of habitat shape, connectivity, aggregation and heterogeneity that were independent of LLI, based on an analysis of artificial multi-class neutral landscapes (With & King 1997) using a modified version of SIMMAP 2.0 (Saura & Martínez-Millán 2000) (see Appendix S5 for further detail). Final landscape metrics were orthogonal to LLI scores as well as to one another and quantified three aspects of configuration independent of area: (1) perimeter-area ratio distribution (PARA_MN, mean patch shape and edge density), (2) Euclidean nearest neighbour distance distribution (ENN_CV, variation in interpatch connectivity) and (3) interspersion and juxtaposition index (IJI, patch aggregation).

Statistical analyses

We analysed the influence of local and landscape factors on empirical wild bee abundance and richness using general linear mixed-effects models with Gaussian error distribution. Following Williams *et al.* (2010), we predicted each pollinator response variable (abundance and richness) based on the general model structure: $E(a, r) = e^{\beta 0}e^{\beta X} \rightarrow \ln[E(a,r)] = \beta_0 + \beta_i X_i$, where E(a, r) is expected wild bee abundance or richness, X_i are the covariates (local and landscape variables) and covariate interactions, β_i are the partial regression coefficients for each i covariate and interaction and β_0 is the expected value when covariates are null. As some sites had values of abundance and richness equal to zero, we transformed responses by ln [a + 1, r + 1]. Residuals of fitted models were approximately normally distributed with no strong pattern of overdispersion or heteroscedasticity (see Appendix S6 for further information). We modelled total, social and solitary bee abundance and richness across all studies and total abundance and richness in tropical and subtropical (collectively referred to as tropical), Mediterranean and temperate studies separately to assess potential differences by biome.

To account for interstudy differences in methods and sampling units and for correlation of fields sampled across multiple years, we included additive random effects for the intercept with respect to both study and site-within-study. Our models estimated different intercepts per study to account for the hierarchical data structure and differences among crop systems, which has been found to be effective for cross-study syntheses (Stram 1996; Gelman & Hill 2007). By modelling an exponential relationship between bee responses and covariates, coefficients estimated proportional changes in responses as a function of covariates (see Ricketts *et al.* 2008; Williams *et al.* 2010). Even though intercepts were allowed to vary for each study, we modelled a common slope (β_i) given our goal of quantifying a general relationship to local and landscape variables across crop systems. To interpret the main effects in the presence of interactions, we mean-centred continuous covariates (Gelman & Hill 2007; Schielzeth 2010).

We developed a candidate model set to test fixed effects. Our global model included all main effects and all two-way interactions between landscape composition (LLI), field type (FT) (conventional vs. organic) and field-scale diversity (FD) (locally simple vs. locally diverse) and between LLI, FT, and FD with landscape configuration (PARA_MN, ENN_CV, IJI). Our candidate set included 135 models, and was balanced such that each of the six covariates appeared in 88 models (Table S6_1).

We ranked competing models based on AICc, identified top models (i.e. ΔAICc from the best model < 2.0) for each response variable, and calculated associated Akaike weights (*w*) (Burnham & Anderson 2002). To assess local and landscape effects, we calculated model-averaged partial regression coefficients for each covariate based on the 95% confidence set (Burnham & Anderson 2002). We determined the relative importance of each covariate based on the sum of Akaike weights across the entire model set, with 1 being the most important (present in all models with weight) and 0 the least important. Covariates were considered important if they appeared in top models (ΔAICc < 2.0) and had a relatively high summed Akaike weight ($w > 0.6$). We report 95% confidence intervals (CIs) around model-averaged partial slope coefficients (β_i) for aggregated studies and 90% CIs for biome-specific analyses (due to reduced sample sizes) and deemed an effect significant if unconditional CIs did not include zero. Statistical analyses were performed using the *R* statistical system v 2.11.1 (R Development Core Team 2008); model selection for mixed models was conducted using 'lme4' package (Bates *et al.* 2008) and 'MuMIn' package for model-averaging of coefficients (Barton 2011).

RESULTS

A total of 675 bee taxa were modelled using the Lonsdorf *et al.* (2009) model, with an average of 52 (± 27 1 SD) taxa per study (Table 1). Per field site, average total bee richness was ~7 (± 6 1 SD) and average total abundance was ~56 (± 144 1 SD) (Appendix S7, Table S7_1). Social and solitary species were roughly equally represented across studies (social bees represented 47% of total abundance).

Across all studies, abundances of wild bees were best predicted by field type (conventional vs. organic), field-scale diversity (locally simple vs. locally diverse; both variables with $w \geq 0.99$ for total, social and solitary bees) and Lonsdorf landscape index (an ecologically scaled index of landscape composition) ($w = 1.00$ for total and social bees, and 0.74 for solitary bees) (Table 2). These three covariates were included in the most supported models (ΔAICc < 2.0) with the highest Akaike weights (Table S7_2). Based on main effects, and holding other variables constant at their average value, total bee abundance and social bee abundance across all studies increased on average by 36.6 and 33.8%, respectively, for each 0.1 unit increase in LLI (or by an estimated factor of 22.6 and 18.4, respectively, with LLI increasing from 0 to 1) (Fig. 1a, c), whereas solitary bee abundances were estimated to increase by 5.1% per 0.1 unit increase in LLI (or by a factor of 1.64 with LLI increasing from 0 to 1) (Fig. 1e). For local-scale effects, abundances of total bees, and of solitary and social species were on average higher when fields had a diversity of crops or non-crop vegetation (76.3, 73.5 and 61.6% respectively) and when managed organically (74.0, 72.8 and 45.2%, respectively; 95% CIs > 0 in all cases) (Table 2, Fig. 1; Figure S7_1). Effects of landscape configuration on bee abundance were weak, with lower summed Akaike weights (total, $w = 0.30$–0.40; social, $w = 0.67$–0.97; solitary, $w = 0.14$–0.16), and model-averaged partial slope coefficients near 0. Variation in interpatch distance (i.e. ENN_CV), however, was predicted to cause 3% declines in social bee abundance per 10% increase in ENN_CV ($w = 0.97$, 95% CIs not overlap zero) (Table 2).

Similarly, wild bee richness was strongly determined by LLI and organic vs. conventional management but to a lesser extent field-scale diversity for total, social and solitary bees ($w \geq 0.92$) across all studies (Table 2). Total bee richness and social bee richness increased significantly on average by 38.0 and 29.7% per 0.1 unit increase in LLI (or by a factor of 25.0 and 13.5, respectively, with LLI changing from 0 to 1) (Fig. 1b, d), and solitary bee richness increased by 8.7% per 0.1 increase in LLI (or a factor of 2.3 with a change in LLI from 0 to 1) based on point estimates only (Fig. 1f). Average richness of total, solitary and social species was significantly higher on organic than conventional fields by 49.9, 48.1 and 28.5% respectively; however, only solitary bee richness was significantly (28.0%) higher in locally diversified fields (Table 2). Bee richness did not respond strongly to landscape structure (low Akaike weights and 95% CIs including zero), but all three configuration metrics (PARA_MN, ENN_CV and IJI) appeared in some of the top models for social bee richness (Table S7_2).

When studies were analysed by biome, LLI had a positive effect on both bee abundance and richness in tropical and Mediterranean systems ($w > 0.99$), causing an average increase of 23.2 and 35.5% in tropical and 128.9 and 41.1% in Mediterranean, respectively, for each 0.1 unit increase in LLI (Table 3, Fig. 2). LLI did not significantly affect bees in temperate studies, where field type was the dominant factor ($w = 1.00$) (Table 3). In both Mediterranean and temperate systems, organic fields were estimated to harbour 67.7 and 41.5% higher bee abundance and 56.1 and 43.8% higher bee richness than in conventional fields (Fig. 3). Across all biomes, habitat aggregation (as measured by IJI) had the greatest influence of configuration metrics ($w > 0.80$ for all bee responses except tropical richness, and appearing in all top models) (Table 3, Table S7_2).

We found some evidence of interactions between local and landscape factors, which were stronger and better supported for richness than for abundance (Table 2, Appendix S7). The average influence of LLI on bee richness and abundance decreased when fields were diversified and managed organically; however, the only significant interaction was between LLI and field-scale diversity for total bee richness across all studies (Table 2). For each 0.1 unit increase in LLI, total bee richness and abundance was estimated to increase in locally simple (monocultural) fields by 32.0 and

Table 2 Model-averaged partial regression coefficients and unconditional 95% CIs from models of total, social and solitary wild bee abundance and richness (n = 39 studies) in relation to local and landscape factors (model set in Appendix S5). Coefficients are based on log-transformed data and in bold where CIs do not include 0. Akaike weights (w_j) indicate relative importance of covariate j based on summing weights across models where covariate j occurs. LLI = Lonsdorf landscape index (an ecologically scaled index of landscape composition); FT = Field type (conventional vs. organic); FD = Field-scale diversity (locally simple vs. locally diverse); PARA_MN = perimeter-area ratio distribution; ENN_CV = Euclidean nearest neighbour distance distribution; and IJI = interspersion & juxtaposition index

	Total bee abundance				Social bee abundance				Solitary bee abundance			
Covariate	w	$\hat{\hat{\beta}}$	Lower CI	Upper CI	w	$\hat{\hat{\beta}}$	Lower CI	Upper CI	w	$\hat{\hat{\beta}}$	Lower CI	Upper CI
Lonsdorf landscape index (LLI)	1.00	**3.1200**	**1.4600**	**4.7800**	1.00	**2.9100**	**1.3000**	**4.5100**	0.74	0.4930	−1.0200	2.0100
Field type-organic (FT)	1.00	**0.5540**	**0.2670**	**0.8410**	0.99	**0.3730**	**0.1260**	**0.6190**	1.00	**0.5470**	**0.2950**	**0.7990**
Field diversity-complex (FD)	1.00	**0.5670**	**0.2490**	**0.8850**	0.99	**0.4800**	**0.1630**	**0.7970**	1.00	**0.5510**	**0.2510**	**0.8520**
PARA_MN	0.30	0.0000	−0.0004	0.0004	0.67	0.0000	−0.0007	0.0006	0.16	−0.0001	−0.0004	0.0003
ENN_CV	0.40	−0.0006	−0.0026	0.0014	0.97	**−0.0030**	**−0.0055**	**−0.0005**	0.14	0.0000	−0.0008	0.0008
IJI	0.33	0.0008	−0.0033	0.0048	0.73	0.0026	−0.0037	0.0089	0.14	−0.0002	−0.0025	0.0022
LLI:FT	0.21	−0.1840	−1.4900	1.1200	0.05	−0.0006	−0.5320	0.5310	0.59	−1.5700	−4.6000	1.4700
LLI:FD	0.25	−0.3840	−2.3000	1.5300	0.07	−0.1220	−1.2700	1.0300	0.23	−0.2700	−1.9100	1.3700
FT:FD	0.34	−0.1160	−0.5200	0.2880	0.05	−0.0098	−0.1450	0.1250	0.26	−0.0317	−0.3110	0.2480
LLI:PARA_MN	0.02	0.0000	−0.0008	0.0007	0.05	0.0000	−0.0012	0.0011	0.01	0.0000	−0.0005	0.0005
LLI:ENN_CV	0.02	0.0001	−0.0023	0.0025	0.12	−0.0013	−0.0098	0.0072	0.00	0.0000	−0.0012	0.0012
LLI:IJI	0.01	0.0001	−0.0081	0.0083	0.06	0.0019	−0.0211	0.0249	0.00	0.0000	−0.0047	0.0047
FT:PARA_MN	0.02	0.0000	−0.0001	0.0001	0.09	−0.0001	−0.0005	0.0004	0.00	0.0000	0.0000	0.0000
FT:ENN_CV	0.02	0.0000	−0.0007	0.0006	0.10	−0.0003	−0.0026	0.0020	0.00	0.0000	−0.0002	0.0002
FT:IJI	0.01	0.0001	−0.0021	0.0023	0.08	0.0010	−0.0070	0.0090	0.00	0.0000	−0.0009	0.0009
FD:PARA_MN	0.02	0.0000	−0.0002	0.0001	0.06	0.0000	−0.0003	0.0002	0.00	0.0000	0.0000	0.0000
FD:ENN_CV	0.02	0.0000	−0.0007	0.0008	0.08	−0.0001	−0.0018	0.0016	0.00	0.0000	−0.0003	0.0003
FD:IJI	0.02	−0.0001	−0.0020	0.0019	0.06	−0.0003	−0.0049	0.0043	0.00	0.0000	−0.0008	0.0008

	Total bee richness				Social bee richness				Solitary bee richness			
Covariate	w	$\hat{\hat{\beta}}$	Lower CI	Upper CI	w	$\hat{\hat{\beta}}$	Lower CI	Upper CI	w	$\hat{\hat{\beta}}$	Lower CI	Upper CI
Lonsdorf landscape index (LLI)	1.00	**3.2200**	**2.0700**	**4.3600**	1.00	**2.6000**	**1.2400**	**3.9500**	0.92	0.8370	−0.2960	1.9700
Field type-organic (FT)	1.00	**0.4050**	**0.2180**	**0.5920**	1.00	**0.2510**	**0.1070**	**0.3950**	1.00	**0.3930**	**0.2220**	**0.5650**
Field diversity-complex (FD)	0.99	0.0470	−0.1560	0.2500	0.93	−0.0585	−0.2350	0.1180	0.98	**0.2470**	**0.0335**	**0.4600**
PARA_MN	0.23	0.0000	−0.0003	0.0002	0.57	−0.0001	−0.0005	0.0003	0.20	0.0000	−0.0003	0.0002
ENN_CV	0.24	−0.0003	−0.0013	0.0008	0.58	−0.0005	−0.0018	0.0007	0.20	−0.0002	−0.0012	0.0008
IJI	0.23	−0.0001	−0.0019	0.0017	0.56	−0.0002	−0.0028	0.0024	0.19	−0.0001	−0.0019	0.0017
LLI:FT	0.41	−0.3400	−1.5700	0.8880	0.20	0.0579	−0.5830	0.6990	0.81	−1.5300	−3.4500	0.3800
LLI:FD	0.96	**−2.6400**	**−4.5400**	**−0.7310**	0.77	−1.9100	−4.3100	0.5010	0.36	−0.3720	−1.7900	1.0500
FT:FD	0.64	−0.1540	−0.4630	0.1540	0.31	−0.0487	−0.2430	0.1460	0.39	−0.0710	−0.3340	0.1920
LLI:PARA_MN	0.00	0.0000	−0.0001	0.0001	0.15	0.0004	−0.0016	0.0024	0.04	0.0000	−0.0007	0.0006
LLI:ENN_CV	0.00	0.0000	−0.0003	0.0003	0.01	0.0000	−0.0009	0.0009	0.04	0.0000	−0.0017	0.0016
LLI:IJI	0.00	0.0000	−0.0012	0.0012	0.01	0.0003	−0.0070	0.0077	0.04	−0.0017	−0.0200	0.0166
FT:PARA_MN	0.00	0.0000	0.0000	0.0000	0.12	−0.0001	−0.0004	0.0003	0.01	0.0000	0.0000	0.0000
FT:ENN_CV	0.00	0.0000	−0.0001	0.0001	0.01	0.0000	−0.0003	0.0003	0.00	0.0000	−0.0002	0.0002
FT:IJI	0.00	0.0000	−0.0002	0.0002	0.01	0.0000	−0.0012	0.0013	0.01	0.0000	−0.0007	0.0007
FD:PARA_MN	0.00	0.0000	0.0000	0.0000	0.24	−0.0001	−0.0006	0.0004	0.00	0.0000	0.0000	0.0000
FD:ENN_CV	0.00	0.0000	−0.0001	0.0001	0.12	−0.0001	−0.0010	0.0009	0.00	0.0000	−0.0001	0.0001
FD:IJI	0.00	0.0000	−0.0004	0.0004	0.12	0.0000	−0.0024	0.0025	0.00	0.0000	−0.0004	0.0004

5.2% on average, respectively, relative to locally diverse fields (Figure S7_2a). Similar increases caused by LLI were higher by 4.6 and 2.5% for bee richness and abundance, respectively, in conventional fields relative to organic (but in all cases, except for total richness, 95% CIs included 0) (Figure S7_2b). These interactions predict that the marginal increase from higher habitat quality within a landscape is on average less when crop fields are diversified or organically managed. Local farming variables may also interact. Effects of organic farming on bee richness and abundance were reduced by 21.4% (w = 0.64) and 19.1% (w = 0.34) on average when fields were locally diversified (Figure S7_2c) (but again CIs included 0). In tropical crop systems, landscape composition (LLI) and configuration (IJI) had a significant positive interaction, such that a 10% increase in LLI caused average bee abundance to increase about twice as much when IJI = 10 as when IJI = 0 (Table 3, Figure S7_3).

DISCUSSION

Although it is increasingly evident that pollinators can be influenced by both local and landscape characteristics (e.g. Tscharntke *et al.* 2005; Kremen *et al.* 2007; Batary *et al.* 2011; Concepción *et al.* 2012), this study is the first global, quantitative synthesis to test the relative and interactive effects of landscape composition and landscape configuration in combination with local farming practices (conventional vs. organic farming, and field diversity). We found that both landscape- and local-scale factors influenced wild bee assemblages in significant and sometimes interactive ways. At the

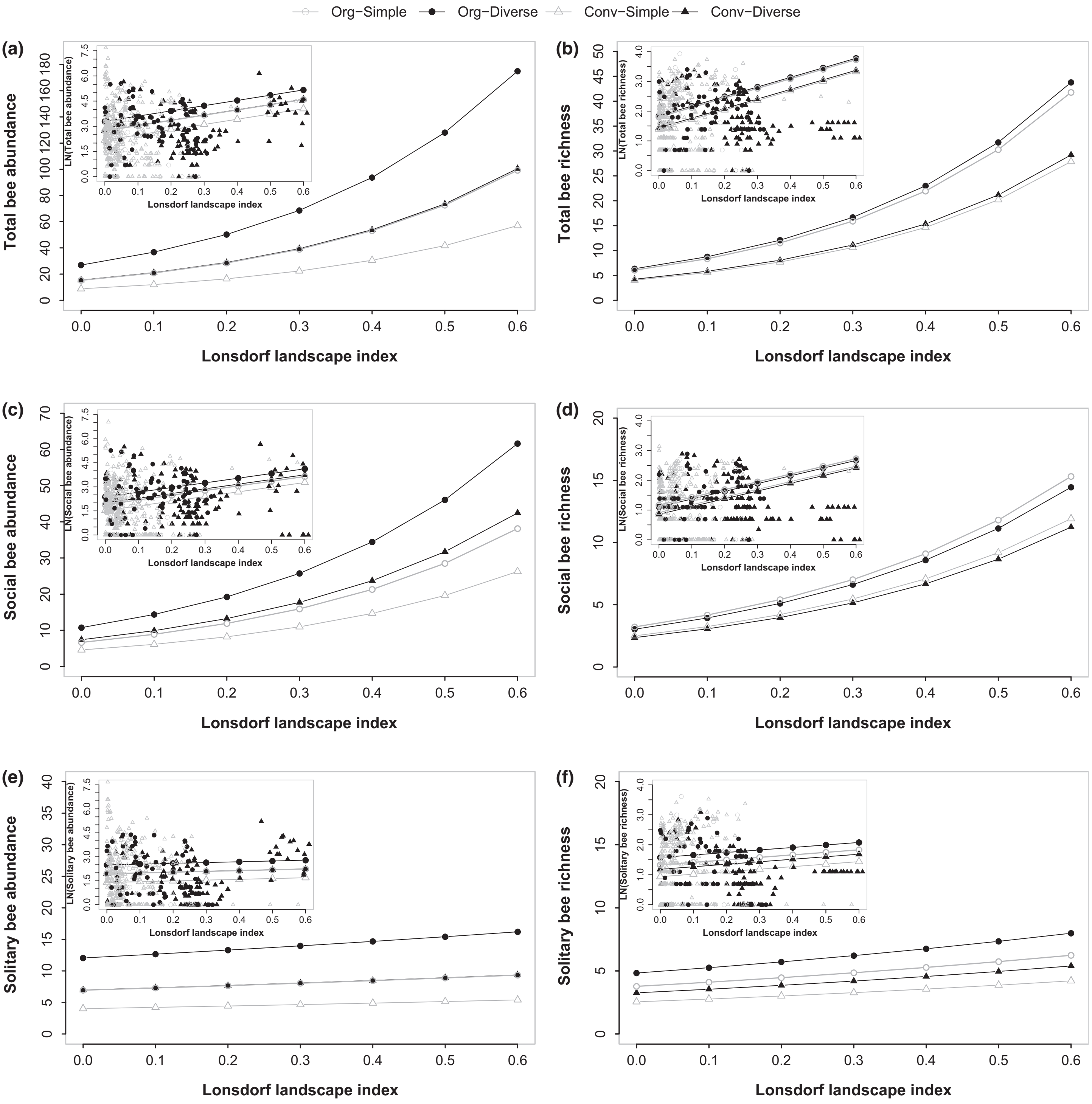

Figure 1 Response to Lonsdorf landscape index of wild bee abundance (a) and richness (b), social bee abundance (c) and richness (d), and solitary bee abundance (e) and richness (f) in relation to field type (conventional vs. organic) and field diversity (locally simple vs. diverse). Estimates are based on model-averaged partial regression coefficients for all studies ($n = 39$) for important main effects [E (abundance, richness) = f (LLI + FT + FD)] (Table 2). Predicted relationship based on back-transformed estimates on normal scale in the main graph (with 95% CIs in Figure S7_1) and modelled log-linear relationship with sites in the inset (based on mean values per site, varying intercepts by site and study not shown). *y*-axis scales vary by bee responses; predicted relationships between LLI = 0–0.60 graphed (although maximum LLI = 1.0) because 0.61 was maximum score derived for empirical landscapes.

landscape scale, bee abundance and richness were higher if more high-quality habitats surrounded fields (i.e. higher LLI scores). This effect was most pronounced in Mediterranean and tropical systems (Fig. 2). At the local scale, both organic management and field-level diversity enhanced bee abundance, and organic management enhanced richness (Table 2). When studies were analysed by biome, organic farming was the driving management effect in Mediterranean and temperate crop systems (Table 3, Fig. 3). Divergent regio-

Table 3 Model-averaged partial regression coefficients and unconditional 90% CIs from models of wild bee abundance and richness by biome in relation to local and landscape factors. Coefficients are based on log-transformed data and in bold where CIs do not include 0. Akaike weights (w_j) indicate relative importance of covariate *j* based on summing weights across models where covariate *j* occurs. (See Table 1 for biome definitions, Table 2 for covariate definitions, Appendix S6 for model set and Appendix S7 for summary statistics by biome)

	Bee abundance – tropical/subtropical				Bee abundance – Mediterranean				Bee abundance – temperate			
Covariate	*w*	$\hat{\hat{\beta}}$	Lower CI	Upper CI	*w*	$\hat{\hat{\beta}}$	Lower CI	Upper CI	*w*	$\hat{\hat{\beta}}$	Lower CI	Upper CI
Lonsdorf landscape index (LLI)	1.00	**2.0900**	**0.5310**	**3.6600***	0.99	**8.2800**	**3.1400**	**13.4000***	0.47	0.3980	−1.1000	1.8900
Farm type-organic (FT)	0.40	0.1820	−0.2950	0.6590	0.88	**0.5170**	**0.0701**	**1.0989**	0.99	**0.4450**	**0.1530**	**0.7370***
Field diversity-complex (FD)	0.32	0.1520	−0.3240	0.6280	0.94	1.0000	−0.4430	2.4500	0.86	0.1940	−0.1140	0.5020
PARA_MN	0.44	0.0001	−0.0005	0.0006	0.79	0.0000	−0.0021	0.0022	0.80	−0.0005	−0.0015	0.0004
ENN_CV	0.44	−0.0002	−0.0020	0.0015	0.81	−0.0022	−0.0067	0.0022	0.78	0.0003	−0.0020	0.0026
IJI	0.95	**0.0122**	**0.0018**	**0.0226**	0.82	0.0064	−0.0078	0.0205	0.83	0.0021	−0.0058	0.0100
LLI:FT	0.05	0.1870	−1.8700	2.2400	0.04	0.1420	−2.3000	2.5900	0.08	−0.2320	−1.7600	1.2900
LLI:FD	0.02	−0.0136	−0.8900	0.8630	0.13	−0.5300	−4.6300	3.5700	0.03	0.0063	−0.6280	0.6410
FT:FD	0.01	0.0011	−0.0911	0.0933	0.14	−0.3220	−1.8200	1.1800	0.11	−0.0508	−0.3780	0.2770
LLI:PARA_MN	0.04	−0.0001	−0.0013	0.0011	0.20	0.0059	−0.0266	0.0385	0.05	−0.0005	−0.0040	0.0031
LLI:ENN_CV	0.04	0.0005	−0.0043	0.0053	0.02	0.0024	−0.0320	0.0367	0.03	0.0002	−0.0055	0.0058
LLI:IJI	0.94	**0.1410**	**0.0582**	**0.2250***	0.09	−0.0519	−0.3550	0.2510	0.11	−0.0011	−0.0379	0.0358
FT:PARA_MN	0.02	−0.0001	−0.0009	0.0008	0.29	−0.0012	−0.0052	0.0028	0.06	0.0000	−0.0004	0.0004
FT:ENN_CV	0.02	0.0001	−0.0020	0.0022	0.03	−0.0001	−0.0023	0.0021	0.04	−0.0002	−0.0030	0.0025
FT:IJI	0.23	0.0036	−0.0109	0.0180	0.05	0.0009	−0.0106	0.0124	0.70	−0.0231	−0.0550	0.0089
FD:PARA_MN	0.00	0.0000	−0.0002	0.0002	0.62	−0.0069	−0.0173	0.0034	0.04	0.0000	−0.0002	0.0002
FD:ENN_CV	0.00	0.0000	−0.0004	0.0004	0.12	−0.0016	−0.0104	0.0071	0.04	0.0002	−0.0017	0.0021
FD:IJI	0.09	0.0001	−0.0070	0.0072	0.19	0.0060	−0.0264	0.0383	0.68	−0.0188	−0.0438	0.0062

	Bee richness – tropical/subtropical				Bee richness – Mediterranean				Bee richness – temperate			
Covariate	*w*	$\hat{\hat{\beta}}$	Lower CI	Upper CI	*w*	$\hat{\hat{\beta}}$	Lower CI	Upper CI	*w*	$\hat{\hat{\beta}}$	Lower CI	Upper CI
Lonsdorf landscape index (LLI)	1.00	**3.0400**	**1.6700**	**4.4200***	0.99	**3.4400**	**1.2900**	**5.5900***	0.23	0.1630	−0.7530	1.0800
Farm type-organic (FT)	0.40	0.0837	−0.1520	0.3190	0.97	**0.3470**	**0.1190**	**0.5760***	1.00	**0.3630**	**0.1310**	**0.5950***
Field diversity-complex (FD)	0.41	−0.0078	−0.2620	0.2460	0.91	0.2800	−0.3870	0.9460	0.32	−0.0358	−0.1870	0.1150
PARA_MN	0.28	0.0000	−0.0003	0.0003	0.78	0.0002	−0.0007	0.0011	0.37	−0.0001	−0.0005	0.0003
ENN_CV	0.31	−0.0003	−0.0016	0.0009	0.77	0.0007	−0.0010	0.0024	0.35	−0.0004	−0.0018	0.0010
IJI	0.50	0.0019	−0.0034	0.0072	0.80	0.0009	−0.0061	0.0079	0.81	−0.0018	−0.0069	0.0033
LLI:FT	0.07	0.0798	−0.8550	1.0200	0.07	0.1840	−1.5000	1.8700	0.06	−0.1030	−0.9880	0.7810
LLI:FD	0.25	−0.9180	−3.7600	1.9300	0.22	−0.6910	−3.5100	2.1300	0.05	−0.0872	−0.8970	0.7230
FT:FD	0.05	0.0074	−0.1260	0.1400	0.17	−0.1600	−0.8190	0.5000	0.13	−0.0663	−0.3770	0.2440
LLI:PARA_MN	0.10	0.0004	−0.0018	0.0026	0.05	0.0005	−0.0058	0.0068	0.02	−0.0001	−0.0014	0.0012
LLI:ENN_CV	0.02	0.0000	−0.0009	0.0009	0.01	0.0003	−0.0070	0.0076	0.01	0.0000	−0.0019	0.0020
LLI:IJI	0.36	0.0232	−0.0318	0.0782	0.41	−0.1160	−0.3690	0.1370	0.04	0.0002	−0.0151	0.0154
FT:PARA_MN	0.02	0.0000	−0.0002	0.0002	0.07	0.0001	−0.0006	0.0007	0.06	−0.0001	−0.0006	0.0004
FT:ENN_CV	0.00	0.0000	−0.0004	0.0004	0.03	−0.0001	−0.0011	0.0010	0.01	0.0000	−0.0009	0.0008
FT:IJI	0.02	0.0002	−0.0028	0.0032	0.14	0.0012	−0.0072	0.0096	0.73	−0.0256	−0.0548	0.0036
FD:PARA_MN	0.03	−0.0001	−0.0006	0.0005	0.31	−0.0015	−0.0053	0.0024	0.01	0.0000	−0.0001	0.0001
FD:ENN_CV	0.00	0.0000	−0.0002	0.0002	0.17	−0.0010	−0.0054	0.0033	0.00	0.0000	−0.0003	0.0003
FD:IJI	0.02	−0.0001	−0.0023	0.0021	0.55	0.0128	−0.0130	0.0386	0.11	−0.0012	−0.0080	0.0056

*Unconditional 95% CIs not overlap 0.

nal patterns may have emerged in part due to sampling effects, and should be confirmed through analyses with additional data sets. Overall, in most cases, organic, diverse fields harboured the greatest abundance and richness of wild bees, whereas conventional, simple fields harboured the lowest (Fig. 1, Figure S7_1). Regarding local-landscape interactions, the beneficial effect of surrounding landscape composition on average decreased when fields were multi-cropped or with non-crop vegetation or were managed organically (Table 2, Figure S7_2), but these trends did not necessarily hold on a per biome basis (Table 3), again possibly due to the smaller number of studies per biome.

In contrast, configuration of habitats at a landscape scale had little impact on total bee richness and abundance. Our finding that wild bees are more impacted by the amount of high-quality habitats within bee foraging ranges than by their configuration is consistent with habitat loss being among the key drivers of global pollinator declines (Potts *et al.* 2010a). Nonetheless, we also expected this landscape aspect to influence pollinators given the importance of habitat configuration on species persistence (e.g. Tscharntke *et al.* 2002; Fahrig 2003). Configuration metrics were selected to be orthogonal to LLI scores, precisely to test unique aspects of configuration independent of composition; however, certain configuration effects may already be captured within LLI scores, which include spatial information by weighting the contribution of habitat types by foraging distance (Lonsdorf *et al.* 2009). Of the three configuration metrics examined, we found greatest support for the effects of variation in interpatch distance (ENN_CV) on social bee abundance (Table 2), with slight declines

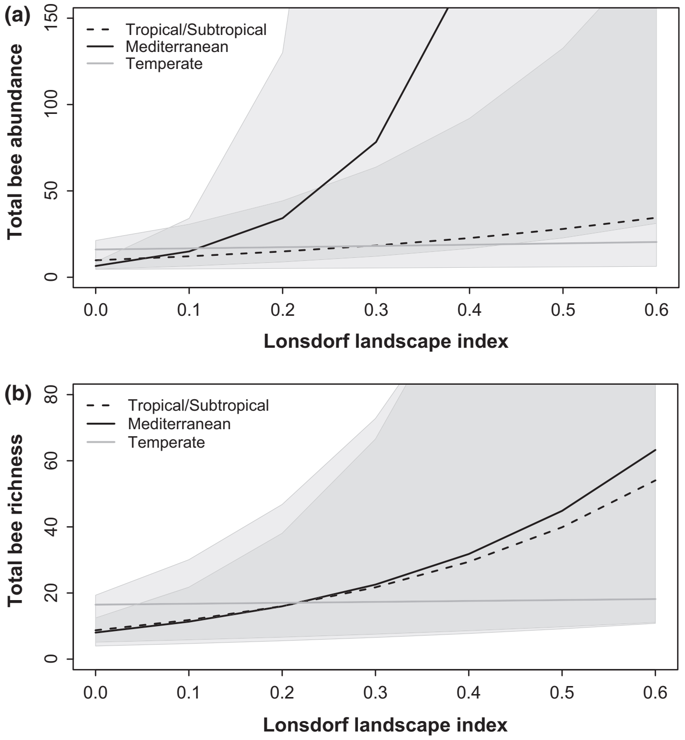

Figure 2 Response to Lonsdorf landscape index (LLI) of wild bee abundance (a) and richness (b) by biome, based on model-averaged partial regression coefficients and unconditional 90% CIs (in Table 3) for tropical and subtropical studies (dashed line for mean) and Mediterranean studies (black line for mean) (grey shading for CIs with dark grey denoting overlapping CIs). Mean effect for temperate studies provided by grey line for reference (CIs not presented due to insignificance). LLI = 0.61 was maximum score observed for tropical landscapes, LLI = 0.19 for Mediterranean landscapes, and LLI = 0.40 for temperate landscapes.

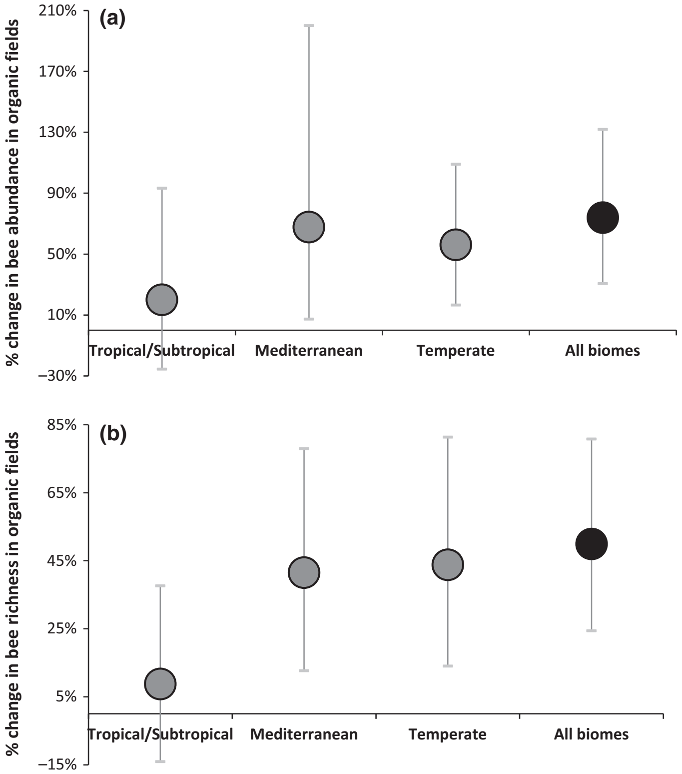

Figure 3 Percent change in wild bee abundance (a) and wild bee richness (b) in organic fields relative to conventional fields for tropical and subtropical studies (n = 10), Mediterranean studies (n = 8), temperate studies (n = 21) and overall (n = 39). Estimates based on model-averaged partial regression coefficients and unconditional 90% CIs by biome and CIs 95% overall (asymmetric CIs due to exponential relationship) (in Tables 2 and 3).

predicted as variation in distance(s) among similar habitat patches increases. In addition, bees in tropical systems had greatest abundance in landscapes with more interspersed high-quality habitats (i.e. both higher IJI and LLI scores) (Table 3, Figure S7_3). Overall, our results did not provide strong evidence for how bees respond to different aspects of landscape configuration (Table 2–3, Table S7_2). Other studies have also found that some bee taxa do not respond to landscape heterogeneity (Steffan-Dewenter 2003) or that they respond idiosyncratically (Carré *et al.* 2009), which may suggest that bees are adequately mobile to tolerate habitat fragmentation as long as the amount of total habitat is sufficient. We note that our assessments of landscape composition and configuration relied in part on expert opinion of suitability of land-cover types as habitat for bees (Appendix S4), with inherent uncertainties and limitations (Lonsdorf *et al.* 2009). Results from this study highlight the need for data on the foraging, nesting, and movement patterns of crop pollinators in different habitat types and landscape contexts.

Increasing agricultural intensification and losses of high-quality habitats can shift pollinator communities to become dominated by common, widespread taxa (e.g. Carré *et al.* 2009). Although we did not model individual bee taxa to discern this type of community shift, we detected differences in responses of social vs. solitary wild bees. Social bees were affected more by landscape effects (LLI and to a lesser extent ENN_CV) than were solitary bees, but both were affected by farm management (Table 2, Fig. 1). Ricketts *et al.* (2008) proposed that specialised nesting requirements, longer flight seasons and foraging distances may predispose social bees to greater sensitivity to habitat isolation. Nesting requirement explanations may not hold in our study because social bees nested in both ground and tree cavities. Although social bees displayed a range of body sizes across studies, 64.7% of our crop systems had bee assemblages in which social species were larger bodied than solitary species, with correspondingly larger foraging distances (by 1.36 times, Greenleaf *et al.* 2007). As a result, social bees may perceive landscapes at larger spatial scales than solitary bees, and thus, be more sensitive to landscape-level habitat structure.

Empirical tests of the assertion that diversified farming systems (i.e. supporting vegetative diversity from plot to field to landscape scales; *sensu* Kremen & Miles 2012) can provide access to different floral and nesting resources over space and time are accumulating. Meta-analyses and multi-region studies on local farm management practices and landscape effects support both scales as important for pollinators. These effects have been found to be additive (Holzschuh *et al.* 2008; Gabriel *et al.* 2010) or interactive (Rundlöf *et al.* 2008; Batary *et al.* 2011; Concepción *et al.* 2012). In the latter case, management interventions – like agri-environment schemes that promote low input, low disturbance farming and the maintenance of field diversity – may be most effective in landscapes with intermediate-levels of heterogeneity (Tscharntke *et al.* 2012).

We found that local management factors have an effect across a wide range of available bee habitats in agroecosystems (Fig. 1), and that both field-scale diversity and organic farming have distinct, positive impacts on wild bee abundance and richness (Tables 2–3). Most striking is that higher vegetation diversity in conventional crop fields may increase pollinator abundance to the same extent as organically managed fields with low vegetation diversity (see also Winfree *et al.* 2008). Local-scale field diversity also increases wild bee richness slightly, although not to the point that it is predicted to match the richness of organic fields (Fig. 1). In some regions, fields under organic management are increasingly becoming large monocultures. Our results suggest that such a trend will ultimately be detrimental for wild bees and their pollination services. Finally, the interactions between local and landscape factors suggest that the local benefits of a diversity of crops or natural vegetation and organic management could transcend an individual field or farm because the improved quality of habitats on one field can provide benefits to adjacent or nearby fields (see also Holzschuh *et al.* 2008). In this way, the distinction between local farm management and landscape effects blur. As a result, the agricultural landscape becomes more of a multifunctional matrix that sustains both crop productivity and natural capital rather than being a single purpose landscape with limited biodiversity value (Perfecto & Vandermeer 2010).

Ultimately, our results suggest that there are several ways to mitigate the negative impacts of agricultural intensification on insect-pollinators, which is generally characterised in many parts of the world by high usage of pesticides and other synthetic chemical inputs, large field size and low (generally monoculture) crop and vegetation diversity (Tscharntke *et al.* 2005; Meehan *et al.* 2011). Reductions in the abundance and richness of wild bees associated with intensive agriculture are thought to result from a combination of lack of floral resources other than mass-flowering crops (Holzschuh *et al.* 2008; Rundlöf *et al.* 2008), lack of nest sites (Williams *et al.* 2010) and high use of pesticides (Brittain *et al.* 2010). In turn, such declines in wild bee communities are expected to lead to reduced pollination services to crops (Klein *et al.* 2009). One mechanism for enhancing pollinator populations is to increase the amount of semi-natural habitat in the landscape (Steffan-Dewenter *et al.* 2002; Kremen *et al.* 2004). Our results suggest that with each additional 10% increase in the amount of high-quality bee habitats in a landscape, wild bee abundance and richness may increase on average by 37%. Such actions, however, are often beyond the capacities of individual producers and can potentially lead to trade-offs between conservation and economic interests. Increasing habitat heterogeneity of agricultural landscapes within the scale of bee foraging ranges is also expected to provide benefits for pollination-dependent crops. Specifically, switching from conventional to organic farming could lead to an average increase in wild bee abundance and richness by 74 and 50%, respectively, and enhancing field diversity could lead to an average 76% increase in bee abundance (Table 2). Potential actions to benefit native bees within farms include reduced use of bee-toxic pesticides, herbicides and other synthetic chemical inputs, planting small fields of different flowering crops, increasing the use of mass-flowering crops in rotations and breaking up crop monocultures with uncultivated features, such as hedgerows, low-input meadows or semi-natural woodlands (Tscharntke *et al.* 2005; Brosi *et al.* 2008). These techniques can be accomplished within fields by individual property owners or managers. The resulting multifunctional landscapes can enhance natural capital and the stocks and flows of other of ecosystem services (e.g. pest regulation, soil fertility, carbon sequestration) in agricultural systems without necessarily diminishing crop yields (Pretty 2008; Kremen & Miles 2012).

CONCLUSION

Our global synthesis expands the growing body of empirical research addressing how changes in landscape structure through habitat loss, fragmentation or degradation affect pollinators and potentially pollination services. We found that the most important factors enhancing wild bee communities in agroecosystems were the amounts of high-quality habitats surrounding farms in combination with organic management and local-scale field diversity. Our findings suggest that as fields become increasingly simplified (large monocultures), the amount and diversity of habitats for wild bees in the surrounding landscape become even more important. On the other hand, if farms are locally diversified then the reliance on the surrounding landscape to maintain pollinators may be less pronounced. Moreover, farms that reside within highly intensified and simplified agricultural landscapes will receive substantial benefits from on-farm diversification and organic management. Safe-guarding pollinators and their services within an agricultural matrix will therefore be achieved through improved on-farm management practices coupled with the maintenance of landscape-level high-quality habitats around farms.

ACKNOWLEDGEMENTS

We thank Nasser Olwero (World Wildlife Fund) for the development of ArcGIS pollinator research tool, J. Regetz (National Center for Ecological Analysis and Synthesis, NCEAS) for guidance on datasets/analyses, E.E. Crone (Harvard University) for statistical consultations and Sharon Baruch-Mordo (The Nature Conservancy) for R graphing code. This study was part of the NCEAS for Restoring Pollination Services Working Group (led by C. Kremen and N.M. Williams, supported by National Science Foundation (NSF) grant no. DEB-00–72909) and by NSF grant no. DEB-0919128 (PIs: CK, EL, MN and NMW). R. Bommarco, M. Rundlöf, I. Steffan-Dewenter, A. Holzschuh, L.G. Carvalheiro and S.G. Potts' contributions were supported in part by 'STEP – Status and Trends of European Pollinators' (EC FP7 grant no. 244090). A.M. Klein's project was supported by the Germany Science Foundation (DFG, KL 1849/4–1), D. Cariveau's project was supported by New Jersey Agricultural Experiment Station through Hatch Multistate Project #08204 to R.W. K. Krewenka and C. Westphal's contributions by the EU FP6 project ALARM (GOCE-CT-2003-506675, http://www.alarmproject.net), H. Gaines and C. Gratton's contributions by University of Wisconsin Hatch Grant WIS01415 and H. Taki's contribution was supported by Global Environment Research Funds (S-9) of the Ministry of the Environment, Japan.

AUTHORSHIP

C.M.K. prepared, modelled and analysed the data and wrote the manuscript; E.L. and M.C.N. assisted with neutral landscape modelling; C.K., E.L., M.C.N. and N.M.W. designed the study, guided analyses and wrote the manuscript; T.H.R. and R.W. consulted on study development; L.A.G. and L.G.C. advised on analyses and revised the manuscript; R.B., C.B., A.L.B., D.C., L.G.C., N.P.C.,

S.A.C., B.N.D., J.H.D., H.R.G., C.G., S.S.G., A.H., R.I., S.K.J., S.J., A.M.K., K.K., Y.M., M.M.M., L.M., M.O., M.P., S.G.P., M.R., T.H.R., A.S., I.S.-D., H.T., B.F.V., R.V., C.W., J.K.W., R.W. and C.K. collected and prepared data and revised the manuscript.

REFERENCES

Aizen, M.A., Garibaldi, L.A., Cunningham, S.A. & Klein, A.M. (2008). Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. *Curr. Biol.*, 18, 1572–1575.

Barton, K. (2011). MuMIn: multi-model inference. R package version 1.0.0. Available at: http://CRAN.R-project.org/package=MuMIn.

Batary, P., Baldi, A., Kleijn, D. & Tscharntke, T. (2011). Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proc. R. Soc. Biol. Sci.*, 278, 1894–1902.

Bates, D., Maechler, M. and Bolker, B. (2011). lme4: linear mixed-effects models using S4 classes. *R Package Version 0.999375-39*. Available at: http://CRAN.R-project.org/package=lme4.

Brittain, C.A., Vighi, M., Bommarco, R., Settele, J. & Potts, S.G. (2010). Impacts of a pesticide on pollinator species richness at different spatial scales. *Basic Appl. Ecol.*, 11, 106–115.

Brosi, B.J., Armsworth, P.R. & Daily, G.C. (2008). Optimal design of agricultural landscapes for pollination services. *Conserv. Lett.*, 1, 27–36.

Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn.. Springer Science + Business Media, LLC., Fort Collins, CO.

Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Crips, J. *et al.* (2009). Landscape context and habitat type as drivers of bee diversity in European annual crops *Agriculture. Ecosyst. Environ.*, 133, 40–47.

Concepción, E.D., Diaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y. *et al.* (2012). Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. *J. Appl. Ecol.*, 49, 695–705.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.*, 34, 487–515.

Gabriel, D., Sait, S.M., Hodgson, J.A., Schmutz, U., Kunin, W.E. & Benton, T.G. (2010). Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecol. Lett.*, 13, 858–869.

Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A. *et al.* (2011). Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.*, 14, 1062–1072.

Gelman, A. & Hill, J.K. (2007). *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, Cambridge, UK.

Greenleaf, S., Williams, N., Winfree, R. & Kremen, C. (2007). Bee foraging ranges and their relationships to body size. *Oecologia*, 153, 589–596.

Holzschuh, A., Steffan-Dewenter, I. & Tscharntke, T. (2008). Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos*, 117, 354–361.

Kearns, C.A., Inouye, D.W. & Waser, N.M. (1998). Endangered mutualisms: the conservation of plant-pollinator interactions. *Annu. Rev. Ecol. Syst.*, 29, 83–112.

Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. *et al.* (2007). Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc.*, 274, 303–313.

Klein, A.M., Mueller, C.M., Hoehn, P. & Kremen, C. (2009). Understanding the role of species richness for pollination services. In: *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective* (eds Bunker, D., Hector, A., Loreau, M., Perrings, C. & Naeem, S.). Oxford University Press, Oxford, pp. 195–208.

Kremen, C. & Miles, A. (2012). Ecosystem services in biologically diversified versus conventional farming systems: Benefits, externalities, and trade-offs. *Ecology and Society*, 17, art. 40. DOI: 10.5751/ES-05035-170440.

Kremen, C., Williams, N.M. & Thorp, R.W. (2002). Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl Acad. Sci.*, 99, 16812–16816.

Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P. & Thorp, R.W. (2004). The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol. Lett.*, 7, 1109–1119.

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R. *et al.* (2007). Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol. Lett.*, 10, 299–314.

Lonsdorf, E., Kremen, C., Ricketts, T., Winfree, R., Williams, N. & Greenleaf, S. (2009). Modelling pollination services across agricultural landscapes. *Ann. Bot.*, 103, 1589–1600.

McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002). *FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps*. University of Massachusetts Amherst, MA.

Meehan, T.D., Werling, B.P., Landis, D.A. & Gratton, C. (2011). Agricultural landscape simplification and insecticide use in the Midwestern United States. *Proc. Natl Acad. Sci. USA*, 108, 11500–11505.

Michener, C.D. (2000). *The Bees of the World*. Johns Hopkins Press, Baltimore, Maryland.

Perfecto, I. & Vandermeer, J. (2010). The agroecological matrix as alternative to the land-sparing/agriculture intensification model. *Proc. Natl Acad. Sci. USA*, 107, 5786–5791.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010a). Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.*, 25, 345–353.

Potts, S.G., Roberts, S.P.M., Dean, R., Marris, G., Brown, M.A., Jones, R. *et al.* (2010b). Declines of managed honey bees and beekeepers in Europe. *J. Apic. Res.*, 49, 15–22.

Pretty, J. (2008). Agricultural sustainability: concepts, principles and evidence. *Philos. Trans. R. Soc. Biol. Sci.*, 363, 447–465.

R Development Core Team (2008). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing Vienna, Austria.

Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A. *et al.* (2008). Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.*, 11, 499–515.

Rundlöf, M., Nilsson, H. & Smith, H.G. (2008). Interacting effects of farming practice and landscape context on bumble bees. *Biol. Conserv.*, 141, 417–426.

Saura, S. & Martínez-Millán, J. (2000). Landscape patterns simulation with a modified random clusters method. *Landscape Ecol.*, 15, 661–678.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.*, 1, 103–113.

Steffan-Dewenter, I. (2003). Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conserv. Biol.*, 17, 1036–1044.

Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C. & Tscharntke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, 83, 1421–1432.

Stram, D.O. (1996). Meta-analysis of published data using a linear mixed-effects model. *Biometrics*, 52, 536–544.

Tallis, H.T., Ricketts, T., Guerry, A.D., Nelson, E., Ennaanay, D., Wolny, S. *et al.* (2011). *InVEST 2.1 beta User's Guide: Integrated Valuation of Ecosystem Services and Tradeoffs*. Natural Capital Project Stanford, Palo Alto, CA, p. 260.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A. & Thies, C. (2002). Characteristics of insect populations on habitat fragments: a mini review. *Ecol. Res.*, 17, 229–239.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.*, 8, 857–874.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batary, P. *et al.* (2012). Landscape moderation of biodiversity patterns and processes – eight hypotheses. *Biol. Rev.*, 87, 661–685.

Vos, C.C., Verboom, J., Opdam, P.F.M. & Ter Braak, C.J.F. (2001). Toward ecologically scaled landscape indices. *Am. Nat.*, 157, 24–41.

Westrich, P. (1996). Habitat requirements of central European bees and the problems of partial habitats. In: *The Conservation of Bees* (eds Matheson, A., Buchmann, S.L., O'Toole, C., Westrich, P. & Williams, I.H.). Academic Press, London, pp. 1–16.

Williams, N.M. & Kremen, C. (2007). Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecol. Appl.*, 17, 910–921.

Williams, N.M., Crone, E.E., Roulston, T.H., Minckley, R.L., Packer, L. & Potts, S.G. (2010). Ecological and life-history traits predict bee species responses to environmental disturbances. *Biol. Conserv.*, 143, 2280–2291.

Winfree, R., Griswold, T. & Kremen, C. (2007a). Effect of human disturbance on bee communities in a forested ecosystem. *Conserv. Biol.*, 21, 213–223.

Winfree, R., Williams, N.M., Dushoff, J. & Kremen, C. (2007b). Wild bees provide insurance against ongoing honey bee losses. *Ecol. Lett.*, 10, 1105–1113.

Winfree, R., Williams, N.M., Gaines, H., Ascher, J.S. & Kremen, C. (2008). Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *J. Appl. Ecol.*, 45, 793–802.

With, K.A. & King, A.W. (1997). The use and misuse of neutral landscape models in ecology. *Oikos*, 79, 219–229.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecology-letters.com).

Editor, Marti Anderson
Manuscript received 29 August 2012
First decision made 9 October 2012
Manuscript accepted 10 January 2013