Title
Assessing the Ability of Habitat Enhancements in Agricultural Fields to Support Native Bee Nesting, Foraging and Ecosystem Services

Author
Sardiñas, Hillary

Publication Date
2015

Assessing the Ability of Habitat Enhancements in Agricultural Fields to Support Native Bee Nesting, Foraging and Ecosystem Services

By

Hillary Suzanne Sardiñas

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:
Chair Professor Claire Kremen
Professor Wayne P. Sousa
Professor Katherine N. Suding

Fall 2015

Abstract

Assessing the ability of habitat enhancements in agricultural fields to support native bee nesting, foraging and ecosystem services

by

Hillary Suzanne Sardiñas

Doctor of Philosophy in Environmental Science, Policy and Management

University of California, Berkeley

Professor Claire Kremen, Chair

Crop pollination is an essential ecosystem service predominantly provided by honey bees and native bees. The decline of honey bees due to a variety of maladies, including Colony Collapse Disorder, has prompted increased interest in unmanaged pollinators. Native bees are effective pollinators, but they have specific habitat requirements, namely floral and nesting resources, that can limit their distribution in agricultural landscapes. This dissertation examines how floral availability and nesting habitat influence pollinator communities and pollination services from native bees.

Increasing floral diversity and abundance has been shown to increase native bee richness and abundance, therefore field-scale habitat enhancements, such as hedgerows, have been proposed as a way to attract and support native bee populations. Whether native bees also visit adjacent crop fields, heightening yields, is less well known. I assess the contribution of native bees visiting hedgerows to seed set in cultivated sunflower, a mass-flowering pollinator-dependent crop (Ch. 1). I find that while sunflower specialist bees (bees that forage exclusively on sunflower) are increased in hedgerow plantings, crop pollination in fields adjacent to hedgerows is not increased. Wild bees, however, both directly and indirectly contribute to sunflower seed set though higher richness and through interactions with honey bee crop visitors.

Factors influencing nest-site selection are less well understood, particularly at the community level. Nest locations are challenging to find; therefore proxies have emerged as a means of correlating potential resources to bee species present in a study area. This approach may overestimate nesting bees; therefore I test a method to randomly sample bee nesting using emergence traps, then determine whether nesting proxies correlate to nesting rates (Ch. 2). Emergence traps are effective at capturing bees in their nests. When I compare bees collected in emergence traps to the community of bees found visiting within site floral resources, I see distinct differentiation between the species collected, indicating that bees foraging within a location may not be nesting there. I find that some proportion of bare ground and variability in slope are strongly correlated to nesting incidence and abundance.

I use the emergence trap technique to examine whether hedgerow field-margin enhancements increase nesting resources and subsequent nesting incidence (Ch. 3). While many nesting

resources are elevated in hedgerow plantings, I find that this does not translate into increased rates of nesting. This could be attributable to the low site coverage provided by emergence traps, or could indicate that the nesting proxies I am evaluating are not strongly indicative of nesting quality.

Models of pollination services in agricultural landscapes estimate floral and nesting resources. These parameterizations are combined with pollinator foraging ranges to generate predictions of pollination coverage. Nesting suitability is primarily based on expert opinion, which in past studies limited potential nest site availability to field margins. I test this assumption in Ch. 4 by sampling with emergence traps in sunflower fields and along field edges. I then combine this nesting data with direct measurements of foraging distances to simulate pollination within a single crop field. I find that while some bees nest directly within crop fields, in the presence of a mass-flowering crop they only forage a small fraction of their foraging range. Pollination services are thus centralized around nest locations.

While increasing floral resources is important for sustaining native bee populations, I do not find a strong effect of hedgerow restorations on pollination of adjacent crops or on nesting resources. Hedgerows may be more effective in different crop or landscape contexts. Because selected bees nest within crop fields, focusing on management of cropped areas, not just field edges, will likely benefit native bees in agricultural landscapes. In order to sustain pollinator populations and maintain agricultural yields, I suggest incorporating multiple methods of diversification into agricultural landscapes.

Dedication

I dedicate this dissertation to my daughter, Nylea Luna, whose impending birth was an incredibly potent motivator and inspiration for writing. Since you've arrived in this world, your curiosity and joy has helped remind me why I went into the fields of conservation biology and restoration ecology in the first place: to protect and improve the environment for future generations. I can't wait to share my love of botany and bees with you on countless hikes together.

Acknowledgements

Claire Kremen was an incredibly supportive advisor, challenging me to become a capable problem-solver and nurturing my enthusiasm for outreach and extension. I wouldn't have gotten through without your guidance.

My lab mates consistently provided feedback, insight and assistance staying on track. You helped me believe in myself and keep pushing forward. Thank you Leithen, Lora, Amber, Alex, Adrian, Emily, Dave, Danny, Cause and Becky! A special thanks to Lauren for stoking my interest in statistics (Rrrrrrr).

Lab managers make sure things don't fall apart. They were always there, thinking of everything I would otherwise forget, making sure field and lab work happened in a timely and comprehensive manner. I am forever indebted to Kerry Cutler, the only person I've ever known to get excited about wasp genitalia, and Sarah Kaiser, for always keeping her cool.

Robbin Thorp is the most generous and dedicated entomologist I know. Thank you for helping me with my IDs. You are a bee hero! Thank you to Rachael Long for your long-standing work on hedgerows— your work makes the Central Valley a better place for bees.

The farmers I worked with were so generous and genuinely excited about the research. Thanks for letting me study on your farms year after year! I also appreciate the support of numerous anonymous sunflower companies, particularly assistance finding farms to do my work on.

My family has always been there for me, cheering me on whatever my pursuits. This continuous support gave me the confidence to initially decide to pursue a PhD and later the strength to persevere through six years of research and analysis. Thank you to my mother, Marsha, my father, Chris, and my sister, Juliet, for always believing in me!

My husband, Jamie, can describe my research project more succinctly and in a more engaging way than I can. He's been there through my ups and downs, always providing perspective and reminding me to enjoy the other parts of my life. Your delicious meals ("brain food") helped push me to the finish line. You're the best! I love you!

Introduction

Pollination is a critical component of the crop production cycle, directly contributing to reproductive success of pollinator-dependent crops. Sufficient pollination enhances seed quantity and quality, which impacts both marketability and profitability (Vaissiere et al. 2011). Seventy – five percent of agricultural crops require or benefit from pollination (Klein et al. 2007), and over the past 50 years, agriculture has become increasingly reliant on pollinator-dependent crops (Aizen et al. 2009). Bees (Hymenoptera: Apoidea) are the most important crop pollinators (Kearns et al. 1998; Garibaldi et al. 2013), providing an estimated $200 billion in pollination services worldwide (Gallai et al. 2009). However, drastic declines in honey bee (*Apis mellifera)* populations due to Colony Collapse disorder and other factors have demonstrated the risk of relying on a single pollinator (vanEngelsdorp et al. 2010). Pollination from unmanaged, native bees (hereafter “wild” bees) has the potential to increase resilience to variability in honey bee supply (Winfree et al. 2007).

Wild bees are capable of providing insurance against fluctuations in honey bee populations (e.g. Greenleaf and Kremen 2006a, 2006b; Winfree et al. 2007; Rader et al. 2009). Wild bees pollinate a wide variety of crops and are often more efficient pollinators than honey bees (Kremen et al. 2004; Morandin et al. 2007; Winfree et al. 2007; Garibaldi et al. 2011; Garibaldi et al. 2013). In addition, interactions between wild bees and honey bees can heighten yields because when different species encounter one another on flowers, they often fly to different locations, causing more pollen to move between different plants (Greenleaf and Kremen 2006a). Some wild bee species, however, have also declined due to agricultural intensification (Kremen et al. 2002). Projected declines of both managed and unmanaged pollinators could cause a 5-8%

decrease in global food production (Aizen et al. 2009). This scenario underscores the necessity of assessing and implementing on-farm strategies that support a diverse, self-sustaining wild bee community.

Heterogeneity at local and landscape scales positively affect wild bee diversity and abundance (Steffan-Dewenter 2002, 2003; Steffan-Dewenter et al. 2002; Klein et al. 2003; Westphal et al. 2003; Kremen et al. 2004a; Garibaldi et al. 2011). In regions where landcover is highly heterogeneous, levels of wild bee pollination remain consistently high across landscape gradients (Winfree et al. 2008). In contrast, when the landscape is homogenous (e.g., California's Central Valley), pollination from wild bees declines as distance from natural habitat increases (Kremen et al. 2004a; Ricketts et al. 2008; Carvalheiro et al. 2010; Garibaldi et al. 2011). In intensive agricultural areas, however, local habitat variables have been shown to be an important factor in augmenting wild bee populations (Greenleaf and Kremen 2006a; Rundlof et al. 2007; Holzschuh et al. 2010; Carvalheiro et al. 2011). Such findings have prompted researchers to suggest that the creation of small-scale, on-farm habitat to promote pollinators (Steffan-Dewenter and Leschke 2003; Kremen et al. 2004, 2007; Tscharntke et al. 2005; Carvell et al. 2008; Holzschuh et al. 2008; Winfree 2010).

Re-diversification of agricultural areas has been proposed as a key tool to bolster pollination services (Kremen and Miles 2012; Kennedy et al. 2013, Garibaldi et al. 2014). Wild bees have two principle needs for successful reproduction: forage (e.g., pollen and nectar) and nesting habitat (e.g., appropriate soil conditions and available nesting resources). To date, the majority of diversification effects have focused on enhancing forage. Hedgerows, linear plantings of native shrubs and forbs, are a common technique that does not take arable land out of production (Menz et al. 2011). Plantings usually contain species with overlapping bloom periods so as to offer sustained resources over time. While this diversification strategy has a demonstrated positive impact on pollinator populations (Kremen et al. 2004; Dixon 2009; Winfree 2010; Garibaldi et al. 2014), few studies have determined whether hedgerows also increase pollination services in adjacent crop fields. Additionally, the ability of hedgerows to increase on-site nest establishment, an indicator of reproductive success, is unknown. This information is critical to determining whether hedgerows are capable of creating self-sustaining populations of wild bees.

Nesting resources are a key predictor of wild bee diversity (Potts et al. 2005; Kremen and M'Gonigle 2015), persistence (Keitt 2009), and response to disturbance (Winfree et al. 2009; Williams et al. 2010). Wild bees are predominantly solitary ground-nesters (Michener 2000), often requiring direct access to open soil. To date, studies of wild bee nesting fall into three main categories: 1) characterization of potential nesting resources (proxies), 2) evaluation of twig-nesting and/or cavity-nesting guilds by providing nesting sites, and 3) evaluation of ground-nesting guilds through trapping bees in their nests.

Identification of potential nesting resources has been used as a proxy for nest detection because the majority of nests are cryptic and therefore difficult to locate. Percent bare ground, percent litter, number of pithy stems, floral abundance and richness, soil hardness and number of potential nesting cavities (cracks or holes in the ground) have been measured and correlated to wild bee diversity and abundance (Potts et al. 2005; Grundel et al. 2010; Morandin and Kremen 2013). While these studies have demonstrated the importance of nesting resources, they have not explicitly linked these resources to nesting incidence; instead they have correlated resources with the community of bees sampled within study sites.

Wild bees present within a site may not be nesting there. Habitats often contain only a portion of the resources bees require to complete their life cycle. This issue, known as the "problem of partial habitats" (Westrich 1996), indicates that simply using presence as an indication of within site nesting is problematic if a bee indeed forages on flowers in one area but nests in another. Zurbuchen et al. (2010) have found that bees will forage greater distances than predicted by their body size in order to visit limited floral resources. Cleared landscapes, including areas with high proportions of agriculture and low amounts of remnant or restored habitat, are resource-poor (Tscharntke et al. 2005). Testing which nesting resources are correlated with nesting bees, and whether foraging bees indeed nest within sites is important in order to form an understanding of the ability of different habitats, including hedgerow restorations, to support bee populations.

In order to sample ground-nesting bee nesting rates it is necessary to capture bees emerging from their nests. The few studies that used ground cover techniques to look at rates of ground-nesting in agricultural landscapes have conflicting findings: Kim et al. (2006) found higher rates of nesting within margins whereas Juiler (2009) detected more nests within fields. The latter study was conducted in squash fields, which have a specialist pollinator, *Peponapis pruinosa* Say, which may preferentially nest in close proximity to its host plant. Conversely, the generalists pollinators found in the former study may not display heightened affinity for nesting near a particular crop. In both studies, the methods utilized to identify nesting bees did not allow for fine-scale detection of nests nor precise correlation with nesting resources. To address these issues, a more targeted technique for sampling nesting incidence in a randomized fashion is warranted. Additionally, these studies compared nesting rates within crop fields to unmanaged margins; they did not assess the ability of hedgerows to increase nesting.

The distribution of floral and nesting resources is used to predict pollination services in agricultural landscapes (Keitt 2009; Lonsdorf et al. 2009; Rands and Whittney 2010; Kennedy et al. 2013). Having accurate assessments of the ability of local-scale floral rediversification, projects such as hedgerows, to impact wild bee nesting is essential to model accuracy, particularly if models are designed to be used to guide agricultural practices. Current models rely on expert opinion combined with landcover data to predict resource rates and nesting suitability of various habitat types. Expert opinion has not been corroborated by data on floral densities nor nesting surveys.

Pollination models also limit bee foraging distance from nest sites by utilizing the range predicted by their body size (Greenleaf and Kremen 2007). Foraging activity, however, may be variable, responding to resource levels. For example, in resource rich areas (such as mass-flowering crop fields) bees may only forage a short distance from their nests, whereas in resource limited areas bees may expand their search range in order to encounter scarce resources (Crone 2013). Testing these foraging predictions in real-world scenarios will also help hone pollination models, contracting or expanding foraging ranges based on floral densities.

This dissertation fills these critical information gaps by examining the extent to which wild bee nesting, and the services they provide to agriculture, can be enhanced through hedgerow restoration. I hypothesized that hedgerows both positively affect yields of adjacent crops and heighten nesting rates. If true, hedgerows would not only enhance models of pollination services but also act as refugia for wild bees, contributing to their conservation in agricultural landscapes. Further, pollination models should ensure that hedgerows be classified as providing suitable floral and nesting resources for wild bees, heightening predicted services in their vicinity. However, if hedgerows do not bolster yields or nesting rates, then models of pollination services need to be re-formulated to exclude them as beneficial habitat, and expert opinion should be rigorously tested in the field. In addition, alternate measures may be required to ensure continued protection of both pollinators and pollination services in intensively farmed areas.

References

Aizen, M.A., L.A. Garibaldi, S.A. Cunningham, A-M. Klein. 2009. How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. *Annals of Botany*, 103: 1579-1588.

Brodt, S., K. Klonsky, L. Jackson, S.B. Brush, and S. Smukler. 2009. Factors affecting adoption of hedgerows and other biodiversity-enhancing features on farms in California, USA. *Agroforestry systems*, 76(1):195-206.

Brosi, B.J., P.R. Armsworth, G.C. Daily, G.C. 2008. Optimal design of agricultural landscapes for pollination services. *Conservation Letters*, 1: 27-36.

Carvalheiro, L.G., C.L. Seymour, R. Veldtman, R. and S.W. Nicolson. 2010. Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *Journal of Applied Ecology*, 47: 810-820.

Carvalheiro, L.G., R. Veldtman, A.G. Shenkute, G.B. Tesfay, C.W.W. Pirk, J.S. Donaldson, and S.W. Nicolson. 2011. Natural and within-farmland biodiversity enhances crop productivity. *Ecology Letters*, 14(3): 251-259.

Carvell, C., W.R. Meek, R.F. Pywell, D. Goulson,and M. Nowakowski. 2006. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, 44: 29-40.

Crone, E.E. 2013. Responses of social and solitary bees to pulsed floral resources. *The American Naturalist* 182(4): 465-473.

Dixon, K.W. 2009. Pollination and Restoration. *Science*, 325: 571-573.

Gallai, N., J-M. Salles, J. Settele, and B.E. Vaissière. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics*, 68: 810-821.

Garibaldi, L.A., M.A. Aizen, S. Cunningham, and A-M. Klein. 2009. Pollinator shortage and global crop yield: Looking at the whole spectrum of pollinator dependency. *Communicative & Integrative Biology*, *2*(1): 37-39.

Garibaldi, L.A., I. Steffan-Dewenter, C. Kremen, J.M. Morales, R. Bommarco, S.A. Cunningham, L.G. Carvalheiro, N.P. Chacoff, J.H. Dudenhöffer, S.S. Greenleaf, A. Holzschuh, R. Isaacs, K. Krewenka, Y. Mandelik, M.M. Mayfield, L.A. Morandin, S.G. Potts, T.H. Ricketts, H. Szentgyörgyi, B.F. Viana, C. Westphal, R. Winfree and A-M. Klein. 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters*, 14: 1062-1072.

Garibaldi, L.A., L.G. Carvalheiro, S.D. Leonhardt, M.A. Aizen, B.R. Blaauw, R. Isaacs, M. Kuhlmann, D. Kleijn, A-M. Klein, C. Kremen, L. Morandin, J. Scheper, and R. Winfree. 2014. From research to action: enhancing crop yield through wild pollinators. *Frontiers in Ecology and the Environment*, 12(8): 439-447.

Greenleaf, S.S. and C. Kremen. (2006a). Wild bees enhance honey bees' pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences*, 103: 13890 -13895.

Greenleaf, S. and C. Kremen. 2006b. Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biological Conservation*, 133: 81-87.

Greenleaf, S., N. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. *Oeclogia*, 153: 589-596.

Grundel, R., R.P. Jean, K.J. Frohnapple, G.A. Glowacki, P.E. Scott, and N.B. Pavlovic. 2010. Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological Applications*, 20: 1678-1692.

Hannon, L.E. and T.D. Sisk. 2009. Hedgerows in an agri-natural landscape: Potential habitat value for native bees. *Biological Conservation*, 142: 2140-2154.

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

Holzschuh, A., I. Steffan-Dewenter, and T. Tscharntke. 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *Journal of Animal Ecology*, 79: 491-500.

Julier, H.E. 2009. Wild bee abundance and pollination service in cultivated pumpkins: Farm management, nesting behavior and landscape effects. *Journal of economic entomology*, 102: 563–573.

Kearns, C.A., D.W. Inouye, and N.M. Waser, N.M. 1998. Endangered Mutualisms: The Conservation of Plant-Pollinator Interactions. *Annual Review of Ecology and Systematics*, 29: 83-112.

Keitt, T.H. 2009. Habitat conversion, extinction thresholds, and pollination services in agroecosystems. *Ecol Appl*, 19: 1561-1573.

Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., R. Bommarco, C. Brittain, A.L. Burley, D. Cariveau, L.G. Carvalheiro, N.P. Chacoff, S.A. Cunningham, B.N. Danforth, J-H. Dudenhöffer, E. Elle, H.R. Gaines, L.A. Garibaldi, C. Gratton, A. Holzschuh, R. Isaacs, S.K. Javorek, S. Jha, A-M. Klein, K. Krewenka, Y. Mandelik, M.M. Mayfield, L.A. Morandin, L.A. Neame, M. Otieno, M. Park, S.G. Potts, M. Rundlöf, A. Saez, I. Steffan-Dewenter, H. Taki, B. Felipe Viana, C. Westphal, J.K. Wilson, S.S. Greenleaf and C. Kremen. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, 16(5): 584-599.

Kim, J., N. Williams, C. Kremen. 2006. Effects of cultivation and proximity to natural habitat on ground-nesting native bees in California sunflower fields. *Journal of the Kansas Entomological Society*, 79: 309-320.

Klein, A-M., B.E. Vaissiere, J.H. Cane, I. Steffan-Dewenter, S.A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of Pollinators in Changing Landscapes for World Crops. *Proceedings of the Royal Society B: Biological Sciences* 274(1608): 303–313.

Klein, A., I. Steffan-Dewenter, T. Tscharntke. 2003. Pollination of Coffea canephora in relation to local and regional agroforestry management. *Journal of Applied Ecology*, 40, 837-845.

Kremen, C., N.M. Williams, and R. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences*, 99: 16812-16816.
Kremen, C., N.M. Williams, R. Bugg, J. Fay, and R. Thorp. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecology Letters*, 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 Letters*, 10: 299-314.

Kremen, C., and A. Miles. 2012. Ecosystem services in biologically diversified versus conventional farming systems: benefits, externalities, and trade-offs. *Ecology and Society*, 17(4), 40.

Kremen, C., and L.K. M'Gonigle. 2015. Small-scale restoration in intensive agricultural landscapes supports more specialized and less mobile pollinator species. *Journal of Applied Ecology*.

Lonsdorf, E., C. Kremen, T. Ricketts, R. Winfree, N.M. Williams, and S. Greenleaf. 2009. Modelling pollination services across agricultural landscapes. *Annals of Botany,* 103: 1589-1600.

Menz, M.H.M., R.D. Phillips, R. Winfree, R., C. Kremen, M.A. Aizen, S.D. Johnson, and K.W. Dixon. 2011. Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. *Trends in Plant Science,* 16: 4-12.

Michener, C.D. 2000. *The bees of the world*. JHU Press.

Morandin, L.A., and C. Kremen. 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications,* 23(4): 829-839.

Morandin, L.A., M.L. Winston, V.A. Abbott, and M.T Franklin, M.T. 2007. Can pastureland increase wild bee abundance in agriculturally intense areas? *Basic and Applied Ecology*, 8: 117-124.

Potts, S.G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, and P. Wilmer. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology,* 30: 78–85.

Rader, R., B.G. Howlett, S.A. Cunningham, D.A. Westcott, L.E. Newstrom-Lloyd, M.K. Walker, D.A.J. Teulon, and W. Edwards. 2009. Alternative pollinator taxa are equally efficient but not as effective as the honeybee in a mass flowering crop. *Journal of Applied Ecology,* 46: 1080-1087.

Rands, S.A., and H.M. Whitney. 2011. Field margins, foraging distances and their impacts on nesting pollinator success. *PloS one*, 6(10): e25971.

Ricketts, T.H., J. Regetz, I. Steffan-Dewenter, S.A. Cunningham, C. Kremen, A. Bogdanski, B. Gemmill-Herren, S.S. Greenleaf, A-M. Klein, M.M. Mayfield, L.A. Morandin, A. Ochieng, and B.F. Viana. 2008. Landscape effects on crop pollination services: are there general patterns? *Ecology Letters*, 11: 499-515.

Roulston, T.H. and K. Goodell. 2011. The Role of Resources and Risks in Regulating Wild Bee Populations. *Annual Review Entomology*, 56: 293-312.

Rundlof, M., H. Nilsson, and H. Smith. 2007. Interacting effects of farming practice and landscape context on bumble bees. *Biological Conservation,* 141(2): 417-426.

Steffan-Dewenter, I. 2002. Landscape context affects trap-nesting bees, wasps, and their natural enemies. *Ecological Entomology,* 27: 631-637.

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

Steffan-Dewenter, I. 2003. Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology,* 17: 1036-1044.

Steffan-Dewenter, I. and K. Leschke. 2003. Effects of habitat management on vegetation and above-ground nesting bees and wasps of orchard meadows in Central Europe. *Biodiversity and Conservation*, 12: 1953-1968.

Tscharntke, T., A-M. Klein, A. Kruess, I. Steffan-Dewenter, C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology Letters,* 8: 857–874.

Vaissiere, B.E., B.M. Freitas, and B. Gemmill-Herren. 2011. *Protocol to detect and assess pollination deficits in crops: a handbook for its use*. UN FAO, Roe, Itlay.

vanEngelsdorp, D., J. Hayes Jr., R.M. Underwood, and J.S. Pettis. 2010. A survey of honey bee colony losses in the United States, fall 2008 to spring 2009. *Journal of apicultural research*.

Westphal, C., I. Steffan-Dewenter, and T. Tscharntke. 2003. Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, 6: 961-965.

Westrich, P. 1996. Habitat requirements of central European bees and the problems of partial habitats. In *Linnean Society Symposium Series* (Vol. 18, pp. 1-16). Academic Press Limited.

Williams, N.M. and C. Kremen. 2007. Resource Distributions among Habitats Determine Solitary Bee Offspring Production in a Mosaic Landscape. *Ecological Applications*, 17: 910-921.

Williams, N.M., E.E. Crone, H.R. T'ai, R.L. Minckley, L. Packer, and S.G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, 143: 2280–2291.

Winfree, R. 2010. The conservation and restoration of wild bees. *Annals of the New York Academy of Sciences*, 1195: 169-197.

Winfree, R., N.M. Williams, J. Dushoff, and C. Kremen, C. 2007. Native bees provide insurance against ongoing honey bee losses. *Ecology Letters*, 10: 1105-1113.

Winfree, R., N.M. Williams, H. Gaines, J. Ascher, and C. Kremen, C. 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology*, 45: 793-802.

Zurbuchen, A., L. Landert, J. Klaiber, A. Müller, S. Hein, and S. Dorn. 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation*, 143(3): 669-676

Chapter 1

Pollination services from field-scale agricultural diversification may be context-dependent

Hillary S. Sardiñas and Claire Kremen

Published in
Agriculture, Ecosystems and Environment
Volume 207, Pages 17-25
September 2015

Abstract

Diversification of field edges is widely used as a strategy to augment pollinator populations and, in turn, supplement crop pollination needs. Hedgerow plantings, a commonly applied field-scale diversification technique, have been shown to increase wild bee richness within edges and into crop fields; however, their effects on pollination services in mass-flowering, pollinator-dependent crops typical of large-scale commercial monocultures are less well-known. We evaluated the indirect contribution of hedgerows to sunflower (*Helianthus annuus*) seed set vis-á-vis wild bee abundance and the interaction between wild bees and managed honey bee pollinators. Although wild bee species richness and the interaction between wild and managed pollinators were significantly associated with augmented seed set, these factors were unrelated to whether a hedgerow was present. The pollinator species foraging within crop fields differed significantly from those found within adjacent hedgerows and bare or weedy field edges, with hedgerows supporting higher species richness than crop fields or unenhanced edges. However, in an independent data set, greater numbers of sunflower-pollinating bees were found in hedgerows than in control edges. Hedgerows may therefore help these crop-pollinating species persist in the landscape. Our findings suggest that hedgerows may not always simultaneously achieve crop pollination and wild bee conservation goals; instead, the benefits of hedgerows may be crop- and region-specific. We recommend evaluation of hedgerow benefits in a variety of crop and landscape contexts to improve their ability to meet ecosystem-service provisioning needs.

Keywords

Apoidea; Ecosystem Services; Hedgerows; Mass-flowering crop; Restoration; Sunflower; Wild bees.

Introduction

Global production of pollinator dependent crops has increased by 300% in the past 50 years (Aizen and Harder 2009). At the same time, managed honey bee (*Apis mellifera* L.) populations are declining due to a complex of factors including novel diseases, pesticides and habitat change (Ellis, Evans and Pettis 2010; Potts et al. 2010; Smith et al. 2013). Pollinator deficiencies may precipitate significant yield reductions and increased food prices, ultimately jeopardizing food security (Meffe 1998; Kevan & Phillips 2001; Steffan-Dewenter et al. 2005; Klein et al. 2007; Gallai et al. 2009). Unmanaged bees (hereafter "wild bees") are highly effective pollinators of a variety of crops and act as insurance against loss of pollination function due to honey bee deficits (Winfree et al. 2007; Garibaldi et al. 2013). While proximity to natural habitat increases populations of such alternate pollinators (Kremen et al. 2002; Ricketts et al. 2008; Kennedy et al. 2013), intensive agricultural landscapes often contain little remnant habitat. As a result, re-diversification of agricultural areas has been proposed as a means of bolstering pollination services from these alternate pollinators (Steffan-Dewenter & Leschke 2003; Kremen et al. 2007; Tscharntke et al. 2005; Brosi et al. 2008; Holzschuh et al. 2008; Winfree 2010; Garibaldi et al. 2014).

Diversification of agricultural landscapes can take place at many scales, including within fields (e.g., polyculture), along field edges (e.g., hedgerows and wildflower plantings), or bordering landscape features (e.g., riparian corridors such as irrigation canals or natural water features; Kremen and Miles 2012). One benefit of field edge techniques is that they create habitat without sacrificing arable land (Menz et al. 2011; Morandin and Kremen 2013), and comprise a large portion of non-cropped area in farming regions globally (Decourtye, Mader and Desnuex 2010). Farm bill conservation programs in the United States and agri-environmental schemes in the European Union prioritize on-farm habitat creation projects that target pollinators, providing incentives through cost-share programs (Vaughn and Skinner 2008). Despite the prominence of these programs, there is little information as to the effectiveness of field-margin diversification techniques, and specifically, whether they can bolster pollinator services and affect yields to the same levels documented in patches of natural habitats (but see Morandin and Kremen 2013; Blaauw and Isaacs 2014) while simultaneously conserving pollinator species (Garibaldi et al. 2014; Kremen and M'Gonigle 2015).

One common field edge diversification technique, hedgerow restoration (linear plantings of native shrubs and forbs), has been found to increase pollinator richness within field edges (Hannon and Sisk 2009; Carvell et al. 2011) and up to 100 m into nearby crop fields (Morandin and Kremen 2013). Additionally, hedgerows show potential for increasing pollination function within adjacent fields. Using sentinel canola plants, Morandin, Long and Kremen (*unpublished data*) found that wild bees enhanced seed set, once the contribution from managed honey bees was accounted for. However, the canola plants provided a highly attractive resource within an unattractive crop matrix of processing tomato, which provides few nectar rewards and requires buzz-pollination to release pollen stores. These conditions are not reflective of the field conditions created by monoculture plantings of pollinator-dependent crops, which generate hundreds of thousands of synchronous, though short-lived, blooms within a single field (known as mass-flowering crops).

Mass-flowering crops (MFCs) can exert strong effects on pollinator populations. Pulses of highly attractive floral resources can create dilution effects, drawing species away from adjacent seminatural habitat and reducing pollination services there (Holzschuh et al. 2011). Yet in spite of the attractiveness of MFC fields, wild bee abundance and richness has been found to be higher in habitats, including hedgerows, in closer proximity to MFC fields (Hanley et al. 2011; Le Feon 2014). The effects of MFCs may be species-specific, with some exhibiting higher preference for MFCs over other resources (Rollin et al. 2013). Specialist pollinators, such as the squash bee (*Peponapis pruinosa* S.), seek out fields of their host plant, cultivated squash, in the landscape (Ullmann and Williams, *in review*). While the influence of MFCs on pollinator populations and services has been well-studied, whether the presence of field-scale restorations can augment pollinator populations and pollination services within MFC fields remains an open question (but see Stanley and Stout 2014).

We examine the ability of hedgerows to enhance pollination services in a simplified agricultural landscape when adjacent to a mass-flowering, pollinator-dependent crop, cultivated sunflower (*Helianthus annuus* L.). We ask whether the identity of the pollinator species found within hedgerows during the crop bloom period is the same as those found within adjacent sunflower fields. Then, using an independent data set, we determine whether the most abundant wild sunflower visitors, sunflower specialist bees, also utilize hedgerow plantings in our study landscape. We also determine whether hedgerow presence affects wild bee abundance and richness in sunflower fields, and if this, in turn, translates into increased sunflower seed set.

Material and methods

Study system

Field sites were located in Yolo County, an intensively-farmed agricultural region of California’s Central Valley that contains a mixture of conventionally managed row and orchard crops. The majority of natural and semi-natural habitat in the county is concentrated around the borders of agricultural lands and not embedded within them (California Department of Water Resources 2008). We sampled 18 sunflower fields between June and July (10 fields in 2012 and 8 fields in 2013). Half of the fields were adjacent to bare or weedy edges (hereafter called controls), and half were adjacent to hedgerows (Fig. S1a). Sites were paired based on the timing of the sunflower bloom, the sunflower variety (specific to company), and landscape context. Field pairs were a minimum of 900 m apart (range, 947- 5,409 m) to maintain independence (Greenleaf et al. 2007). To avoid contamination of varieties, sunflower fields are moved every year; therefore no field was sampled in multiple years although two fields were adjacent to the same hedgerow in different years.

Sunflower

In Yolo Co., acreage planted in sunflower has increased by over 55% during the past 5 years (Yolo County Weights and Measures, Crop Statistics). It is the 8th most-planted crop in the region, grossing nearly $28 million USD in 2013 (Yolo County Weights and Measures, Crop Statistics). It is produced mainly for hybrid seed, which is then grown for oilseed or confection. While sunflower is native to North America, the breeding system of sunflower grown for hybrid seed has been altered to be artificially gynodioecious, with separate male-fertile (nectar and pollen producing; ‘male’) plants and male-sterile (nectar-only producing; ‘female’) plants. For hybrid seed production, rows of male plants are interspersed with rows of female plants. Wild bees predominantly visit male plants to collect pollen for nest provisioning (Parker 1981; Greenleaf and Kremen 2006). Although honey bees visit both male and female plants, workers typically either collect nectar from female plants or pollen from male plants which limits cross-pollination events (Free 1964). Honey bee movement between pollen and nectar producing rows of sunflower is often spurred by interference interactions with wild bees. When a wild bee and honey bee meet on a sunflower head, one or both fly to different sunflower heads or rows (Greenleaf and Kremen 2006; Pisanty et al. 2014). These interactions that increase pollen flow between rows also increase honey bee per visit efficiency, therefore have great potential to heighten seed set (Greenleaf and Kremen 2006; Carvalhiero et al. 2011). Honey bees were stocked at an average rate of approximately 100 hives per field, or 1.5 hives per acre (Greenleaf and Kremen 2006).

We did not evaluate pest management (treated versus untreated fields) because sunflower fields managed by different companies (four main companies) used similar practices. For example, all companies used pre-emergent herbicides prior to planting and seeds were treated with insecticides (Cruiser®, active ingredient: thiamethoxam) and either a fungicide or nematicide. Other management practices, including fertilization, tillage, row width and ratio of male to female rows, are also similar between companies (Long et al. 2011), although irrigation practices vary by field, with the majority using furrow irrigation.

Hedgerows and control edges

Hedgerows were planted by growers to support beneficial insect populations, and include highly similar plant species composition (for more information on hedgerow plantings see Long et al. 1998). Hedgerows were 250-300 m long and 3-6 m wide. During the sunflower bloom period, only a portion of plants in the hedgerow were flowering (Tables S1 & S2). *Eriogonum fasciculatum var. fasciculatum, Heteromeles arbutifolia*, and *Sambucus nigra ssp. cerullea* were the only woody species in bloom. Forbs in bloom included *Achillea millefolium, Asclepias californica, Asclepias fascicularis, Aster chilensis,* and *Grindelia camporum.* Weedy species were present in all hedgerows and most control sites; the dominant species were *Convolvulus arvensis, Brassica* sp., and *Polygonum arenastrum*. Control margins contained only non-native plant species, or were maintained as bare, weed-free areas. Bare/weedy field margins in our study region are managed by burning, herbicides, or scraping; no management actions took place during our study period. By design, hedgerows contained more plant species and more blooms than control weedy edges (Tables S1 & S2).

Landscape context

To quantify the landscape surrounding each site we created 18 land use categorizations (Table S3). We then hand digitized National Agriculture Imagery Program (NAIP) within a 1 km buffer around study sites in ArcGIS 10.1 (Farm Service Agency U.S. Department of Agriculture 2006; ESRI 2011). To determine landscape effects on wild bee populations in sunflower, we examined the proportion of habitat within each buffer that could provide resources to wild bees (hereafter “potential pollinator habitat”). This included both natural habitats (e.g., grasslands, riparian scrub) and altered habitats (e.g., weedy patches, hedgerow restoration). Potential pollinator habitat around our study sites varied from 1- 40%, with a median of 5% (Table S4). Control and hedgerow sites were paired by landscape context to minimize differences.

Sampling methods

We established two 200 m transects within each field, perpendicular to the field edge or hedgerow and 100 m apart (Fig. S1b). We netted and observed pollinators at four distances along these transects: 10, 50, 100 and 200 m from the edge. We varied the starting sampling location within fields and edges at each study site (surveyors started at different starting distances on each transect) to reduce conflation of distance with temporal variation in bee foraging behavior, which peaks in the morning and late afternoon (Pisanty et al. 2014). Each site was sampled once, during peak bloom (> 90% sunflower heads in bloom), on a clear day with wind speeds < 2.5 m/s and temperatures > 18°C between 08:00 h and 14:00 h.

We visually observed visitation for two minutes each in two male-fertile and two male-sterile 2 x 1 m plots at each distance. Within hedgerows and edges we haphazardly sampled floral visitors for two minutes in eighth plots containing floral blooms. Only insects that contacted the anthers or stigmas were recorded as floral visitors. We also recorded non-bee visits; these accounted for <1% of all visits and were, for simplicity, excluded from analyses. We were unable to identify bees to species in visual observations; therefore we classified them to citizen science categories from Kremen et al. (2011; Table S1).

After visual observations were completed, we netted bees visiting male-sterile and male-fertile plants for eight minutes at each distance along each transect, and for 16 minutes along edges. We paused stopwatches during specimen handling. We did not collect *Apis* in netted samples. Specimens were identified by Dr. Robbin Thorp, except *Melissodes spp.*, which were identified by H.S. Sardiñas. Wild bees include both native and non-native non-*Apis* bees. Non-native wild bees, including *Ceratina dallatorreana* and *Megachile apicalis*, make up a small portion (1%) of all records. We did not include feral *Apis* in our wild bee categorization because we were unable to distinguish them from managed *Apis*.

Seed set

To determine ambient pollination rates, we collected three sunflower heads at each distance/transect combination prior to harvest. In the first year of this study we bagged one male-sterile sunflower head at each distance along both transects to determine seed set levels without cross-pollination events. No seeds were produced in any bagged sunflower head, therefore we did not account for seeds set due to selfing in our models of seed set. Heads were dried, measured, and all mature seeds were removed, weighed and counted with a Syntron automatic seed counter. We tested for differences in head size (diameter) between companies using a generalized linear model, with site nested within pair as a random effect, in the R package lme4 (Bates et al. 2013; R version 3.1.2). Sunflower head size was similar between companies (estimated head area 25 cm^2; Table S5), although one company had a wider range of head sizes and was significantly different from the other three companies in the study ($t = -2.22$, $P < 0.05$; Table S5). All hedgerow and control sites were paired by company.

Field edge use by sunflower specialists

Sunflower specialists are more effective pollinators of sunflower than generalist species (Parker 1981; Greenleaf and Kremen 2006). We therefore also investigated whether sunflower specialists were more abundant in hedgerow or control field edges using an independent data set from 26 hedgerows and 21 control edges in Yolo Co. (see Supplement; Fig. S2). Floral visitors were netted for 1 hour in hedgerows and control edges during 4-5 sample rounds between April and August in 2012-13. We queried this specimen database for sunflower specialist bees, which we defined as primary oligoleges (Hurd 1980). To assess whether the amount of nearby sunflower in the landscape impacted sunflower specialist presence in field edges in the independent dataset, we constructed 1 km buffers around sites in ArcGIS 10.4 and recorded the proportion of sunflower fields around each site using pesticide spray records (California Department of Pesticide Regulation), which identify which crop is grown on each parcel, and the California Crop Improvement sunflower isolation map (California Crop Improvement Association).

Statistical analyses

We used a chao estimator to evaluate species richness within sites in the R package vegan (Oksanen et al. 2013). To determine the impact of hedgerow presence, field location (field or edge), and surrounding pollinator habitat in the landscape on wild bee species richness and abundance (from aerial net data) we used general linear models with poisson and negative binomial distributions respectively in the R package lme4 (Bates et al. 2013). Both models included an interaction between hedgerow presence and field location. We used raw species richness because we only sampled each site once and some sites contained too few individuals for estimation or rarefaction (Gotelli and Colwell 2011). We also assessed factors influencing sunflower visitation rates by honey bees and wild bees. Hedgerow presence, distance from hedgerow, and their interaction, potential pollinator habitat, and sunflower sex (male-fertile or male-sterile) were independent variables. In species richness, abundance and visitation models, site nested within pair was included as a random effect.

We evaluated the differences between the community of bees in control edges, hedgerows, and crop fields using a perMANOVA on their Chao1 dissimilarities in the R package vegan (Osaken et al. 2013). We then determined whether male and female sunflower specialist bees utilized hedgerows or control field edges using the independent data set (all other analyses were on the sunflower data). We modeled counts of bees as the dependent variable with a poisson distribution in the R package lme4 (Bates et al. 2013). Hedgerow presence, proportion of sunflower and potential pollinator habitat within a 1 km radius, bee specialization on sunflower, bee sex and an interaction between specialization and hedgerow presence were the independent variables. Site nested within pair was included as a random effect.

To determine which factors impacted sunflower seed set, we used negative binomial generalized linear models in the R package lme4 that accounted for overdispersion in the seed data (Bates et al. 2013). We examined the effect of wild bee abundance and richness on seed set from net and visitation data separately. We used raw species richness because some site-distance combinations contained too few individuals for estimation or rarefaction (Gotelli and Colwell 2011). In all models, sunflower seed set was the dependent variable. In the model for netted bees, independent variables were hedgerow presence, wild bee abundance, wild bee species richness, sunflower company, distance into the field from the edge, and an interaction between netted wild bee abundance and honey bee visitation (based on the observation that honey bees displayed greater per visit pollination efficiency as native bee abundance increased; Greenleaf and Kremen 2006). For the model including visitation rates, additional explanatory variables included aggregate wild bee visitation to male-fertile and male-sterile flowers, honey bee visitation, and an interaction term between wild bee visitation and honey bee visitation. Site nested within pair was included as a random effect in both models.

All continuous variables were scaled ((x – mean)/sd). We checked all variables for collinearity (variance inflation factor < 3; Zuur et al. 2009), and no collinear variables were included in any model. For example, sunflower head size was correlated with variety. However, varieties were specific to sunflower company, so only sunflower company was retained in the model.

Results

Aerial netting

We collected 670 wild bees with aerial netting representing 30 species. Species richness within sites ranged from 0- 3.71, with a mean chao estimated richness of 2. Rarefaction showed that collection of new species was still increasing at a rapid rate (Fig. S3). More species are likely present within the system, although Greenleaf and Kremen (2006) found a similar number of species visiting sunflower in the same study region in fields closer to natural habitat (33 species). We did not net any bees in three control edges that were devoid of floral resources (i.e. managed as bare edges with no weedy species present).

We collected more bees in hedgerow edges than in control edges (Table 1 and Fig 1a). On average, hedgerow edges supported higher species richness (5.11 ± 0.89, mean ± standard error; Fig. 1b) than control edges (2.11 ± 0.48), hedgerow fields (1.41 ± 0.20) or control fields (2.06 ± 0.20; Table 1). We detected a significant interaction between hedgerow presence and location within fields (edge or field) for abundance ($t = -3.91$, $P < 0.001$) and species richness ($t = -4.22$, $P < 0.001$; Fig. S4). Proportion of potential pollinator habitat with a 1 km radius did not influence wild bee species richness ($t = -0.83$, $P = 0.41$) or abundance ($t = -0.49$, $P = 0.62$) within sunflower fields.

Visitation rates

We recorded 2,745 visits to sunflower from wild (339 visits) and honey bees (2,406 visits). We detected 7 times more honey bees visits than wild bee visits ($t = -15.38$, $P < 0.001$; Fig. S5). We did not find a main or interactive effect of hedgerow presence or distance from the edge on visitation rates (Table 1). The amount of pollinator habitat in the surrounding landscape did not affect visitation rates ($t = 1.11$, $P = 0.27$). Confirming past findings (e.g., Greenleaf and Kremen 2006; Parker 1981), we found that wild bees visited male-fertile plants at higher rates (91.4% of visits) than male-sterile plants. Similarly, both honey bees and wild bees visited male-fertile sunflower heads more frequently than male-sterile, seed-producing sunflower heads ($t = 2.56$, $P < 0.05$).

Wild bee habitat use

The communities of bees we found in fields versus edges with aerial netting were strongly differentiated ($F = 4.11$, $P = 0.001$), but the communities found at hedgerow or control edges were not distinct (Fig. 2), despite differences in floral blooms between the edge types (Tables S1 & S2). Bee communities in edges were dominated by generalists (e.g., *Halictus tripartitus*) whereas bee communities in fields contained higher numbers of sunflower specialists (e.g., *Melissodes agilis*; Table S7).

In the independent dataset, we found 627 records of sunflower specialists visiting control and hedgerows edges in 2012-13 (Table S6). Proportion of sunflower within 1 km of study sites ranged from 0 to 0.34. We detected a significant interaction between sunflower specialists and hedgerow presence (Z = 9.79, P < 0.001; Table 2; Fig 3). The majority of sunflower specialists visiting edge habitat were males (87.7%; Z = -26.85, P < 0.001). Specialists visited 16 different plant species, 5 of which were hedgerow plants; the remaining were weedy species (Table S8). 48.8% of all visits were to buckwheat (*Eriogonum fasciculatum*; male bees- 285 visits, female bees- 36 visits).

Fourteen of these sites were adjacent to sunflower in both 2012 and 2013, and the majority of specialist bees were found there (90%), although these were concentrated in 2 hedgerows, which contained 79% of all specimens collected. Proportion of sunflower within a 1 km radius positively affected sunflower specialist presence in field edges (Z = 4.15, P < 0.001). 48 specimens were found in 6 edges that were not adjacent to sunflower, and only 2 of those sites were in close proximity to sunflower fields during previous years. Proportion of potential pollinator habitat in the surrounding landscape did not affect the number sunflower specialists in field edges (Z = -0.98, P = 0.33).

Sunflower seed set

Seed set was affected by netted wild bee species richness (t = 2.05, P = 0.039; Table 3), but not abundance (t = -1.27, P = 0.20). We did not detect an interaction effect between netted wild bee abundance and honey bee visitation rates (Table 3). In the visitation model, the interaction between wild bee and honey bee visitation influenced seed set (t = 2.04, P = 0.041). Neither hedgerow presence nor distance from the field edge impacted sunflower seed set in either the net or visitation models, whereas company strongly affected seed set (Fig. 4).

Discussion

Measuring the levels of ecosystem services derived from field-edge habitat management in a variety of contexts is critical to demonstrating their efficacy and flexibility. If services are highly variable over time or from site to site, costs may outweigh the benefits and limit the adoption of diversification practices (Ghazoul 2007; Hanes et al 2013). Although other studies have found that field-edge diversification increase pollinator populations both in edges and fields (Morandin and Kremen 2013) and enhance pollination services to crops in adjacent fields (Blaauw and Isaacs 2014; Morandin, Long and Kremen, *unpublished data*), we did not detect any differences in rates of seed set in sunflower fields adjacent to hedgerow or control edges. Wild bee richness and an interaction between wild bee visitation and managed honey bee visitation, however, positively impacted seed set; yet these factors were not influenced by hedgerow presence. Proportion of pollinator habitat in the surrounding landscape did not influence the bee community visiting sunflower, despite a large body of evidence supporting strong positive landscape effects (e.g., Ricketts el al. 2008; Kremen et al. 2002). We did find higher numbers of sunflower specialist bees in hedgerows than in control sites. Based on these findings, we conclude that sunflower in not a good candidate crop for field edge enhancements, at least in our study region, although they exhibit potential for supporting populations of sunflower pollinating bees.

We detected distinct differences in community composition of wild bees present in edges versus fields. This difference was likely driven by the fact that the dominant bee species found within fields, sunflower specialists, were either rare visitors to or absent from both hedgerow and control edge habitats. We only sampled each site once, therefore increased sampling could lead to more convergence or divergence between bee communities in these habitats. There can be significant overlap between species found in MFC fields and adjacent hedgerows (Stanley and Stout 2014), however species composition in hedgerows has also been shown to more closely resemble bee communities in forest habitat than adjacent crop fields (Hannon and Sisk 2009). One factor likely driving the differences in species composition in our study region is the absence of sunflower planted within hedgerows due to concerns about genetic contamination of sunflower crop varieties. Because female sunflower specialists collect only sunflower pollen to provision their nests, they may not be attracted to the resources in hedgerows during the sunflower bloom period, instead being drawn into fields (Holzschuh et al. 2011). Nevertheless, assessment of the independent dataset indicated that hedgerows provide important floral resources to sunflower specialist bees, especially males. Male sunflower specialists have been observed investigating honey bees as potential mates, which increases honey bee movement from male-fertile to male-sterile sunflowers and increases their pollination efficacy (Greenleaf and Kremen 2006). Male bees, therefore, likely contribute to the interactive effect between wild bee richness and honey bees on rates of seed set.

We found a slight positive effect of wild bee species richness on seed set rates, indicating that a higher number of bee species benefits pollination function in sunflower. Functional complementarity between species can enhance fruit and seed production in a variety of crops (Hoehn et al. 2008; Blüthgen and Klein 2011). Bee foraging behavior and bee body size can influence within-inflorescence foraging, leading to more complete pollination in a single flower (e.g., strawberry, Chagnon and de Oliviera 1993). Bee foraging activity can also be affected by preferences for particular weather conditions (e.g., almond, Brittain et al. 2013), temperatures (e.g., radish, Albrecht et al. 2012), or preferences for floral phenology (Pisanty et al. 2013) leading to temporal complementarity. Interspecific interactions between bee species can also increase honey bee efficiency (Greenleaf and Kremen 2006; Carvalhiero et al. 2011). In almonds, wild bee presence increases the likelihood that honey bees will move between different rows, which leads to higher pollen tube initiation and subsequent fruit set (Brittian et al. 2013). Both niche complementarity and interspecific interactions likely underlie the positive relationship we detected between richness and seed set (Klein et al. 2009).

In agreement with past findings (Greenleaf and Kremen 2006; Carvalhiero et al. 2011), we detected an interactive effect between wild bee and honey bee visitation on sunflower seed set. We did not, however, detect any main effects of wild bee and honey bee visitation, despite strong evidence that wild bees positively increase seed set regardless of honey bee abundance (Garibaldi et al. 2013). In order to evaluate the direct contribution of wild bees, other studies have estimated the contribution of wild and honey bee visitation to seed set separately (Kremen et al. 2002; Isaacs and Kirk 2010; Winfree, Gross and Kremen 2011; Morandin, Long and Kremen, *unpublished data*). We were unable to do this because of our study design, which did not examine seed set from single bee visits. Nevertheless, this is the first sunflower seed set study to detect an interspecific interactive effect at the community-level rather than at the individual-level. However, despite the importance of these interactive effects on sunflower yield, company was the factor that most strongly influenced seed set. Although there was little variation in head size between sunflower companies (Table S5), using company as a classification may mask other differences, such as genetic differences between varieties and variation in field management techniques. By pairing control and hedgerow sites by company, variety and landscape context, we sought to minimize these potential differences, and the few differences in management practice were noted between companies.

It is hypothesized that the effectiveness of field-edge vegetation re-diversification is maximized in landscapes that retain a small percentage of natural areas that can facilitate recolonization of restored habitats (Tscharntke et al. 2005). The added benefits of diversification efforts may be minimal in complex landscapes with high proportions of natural habitat since ecosystem service providers are often already supported. Diversifcation efforts may not support ecosystem providers in highly intensified (cleared) landscapes with no remaining natural habitat, either because there are no source areas to colonize the new habitats or because the new habitats alone cannot support populations of ecosystem service providers (Tscharntke et al 2013). Although the landscape where we conducted our study constitutes a "cleared" landscape, and we did not detect landscape effects, other studies in the same location have found that hedgerows increase wild bee abundance, richness and population persistence and promote rare and/or more specialized species (Morandin and Kremen 2013; M'Gonigle et al., *in press*, Kremen and M'Gonigle 2015). Nevertheless we did not find evidence that these biodiversity benefits translated into higher rates of pollination services in adjacent sunflower crop fields. Although both wild bee richness and abundance were important factors contributing to sunflower seed set, these contributions may be attributable to factors other than hedgerows. For example, wild bee visitors to sunflower were predominately sunflower specialists; the amount of sunflower maintained in the landscape over time could therefore influence sunflower pollinator populations more strongly than hedgerow plantings that do not contain floral resources suitable for the specialists' dietary requirements (Greenleaf and Kremen 2006), as we found was true in the independent dataset.

It is important to balance the conservation value of field-edge plantings with ecosystem service delivery objectives. While conservation and ecosystem service outcomes can be synergistic, win-win scenarios are challenging to achieve (Naidoo et al. 2008; Tallis et al. 2008). Hedgerows augment pollinator populations, which can be important for achieving wild bee conservation goals (M'Gonigle et al., *in press*; Kremen and M'Gonigle 2015); however, they may not be a "silver bullet" strategy for increasing crop pollination. Both the scale of the re-diversification effort relative to the farming system and the adjacent crop type could limit the effectiveness of hedgerow plantings.

Hedgerows occupy < 1% of our study landscape and contain 175 times less area than a typical average crop field in our study area. The intensity of bloom in hedgerows is also minimal in comparison to the hundreds of thousands of blooms in a single MFC field (Williams, Regetz and Kremen 2012). Increasing the size of hedgerows relative to fields or introducing a suite of diversification techniques could increase the effectiveness of re-diversification efforts (Kremen and Miles 2012). Patch size may influence a habitat's capacity to host different densities of pollinators (Carvell et al. 2011). Alternately, the configuration of habitat could impact pollinator populations. For example, when Morandin and Winston (2006) examined the optimal spatial distribution of a MFC, canola (*Brassica napus*), they found that both profits and pollination services would be maximized if a central field was left fallow or allowed to revert to semi-natural habitat. The size, configuration and quality of habitat may all interact to influence pollinator communities (Garibaldi et al. 2014).

The benefits of field-edge diversifications may also differ based on crop identity and landscape context (Garibaldi et al. 2014). For example, sunflower has easily accessible florets that attract both generalist and specialist pollinators. However, in systems where flowers have specific requirements, such as highbush blueberry (*Vaccinium corymbosum* L.) that requires buzz-pollination, the identity of pollinator species may be of more importance (Button and Elle 2014). Further, species-specific responses to habitat features may differ. Carvell et al. (2011) found bumble bees had differential responses to wildflower patch size and landscape heterogeneity, indicating that local and landscape habitat factors can also interact with one another, and with crop-specific attributes, to affect crop pollination. In a tropical region, Carvalheiro et al. (2012) found that wildflower plantings worked in concert with natural habitat to heighten mango (*Mangifera indica*) production. There are a paucity of studies on the ecosystem service benefits from field-edge plantings, therefore the complex range of factors, including farming type, crop system, landscape context, and region (Holzschuh et al. 2006), influencing their performance is still relatively unknown (Garibaldi et al. 2014).

Conclusion

While hedgerow plantings show promise for augmenting pollinator populations in edge habitats and pollination services in some crop types, benefits from hedgerows likely vary in different cropping systems and landscapes. This context-dependency presents a challenge for promoting hedgerows as a “silver-bullet” strategy to enhance crop pollination. Different crops may require alternate diversification methods or changes in hedgerow design in order to attract pollinators and achieve pollination increases in adjacent crop fields. In intensively-managed (“cleared”) landscapes, hedgerows alone may not be sufficient to promote pollinator populations, and other diversification techniques may be needed to complement hedgerows, such as reducing field size and increasing crop heterogeneity, using more varied crop rotations, etc. (Kennedy et al. 2013; Kremen and Miles 2012). To maximize the efficacy of farm-scale re-diversification techniques, it is important to continue examining the levels of pollination services delivered from farm-scale re-diversification techniques to a variety of crops in a variety of regions. Field-scale interventions can then be targeted to crops and regions where they will have the highest impact.

References

Aizen, M.A., and L.D. Harder. 2009. The Global Stock of Domesticated Honey Bees Is Growing Slower Than Agricultural Demand for Pollination. Current Biology 19 (11): 915–918.

Albrecht, M., B. Schmid, Y. Hautier, and C.B. Müller. 2012. Diverse Pollinator Communities Enhance Plant Reproductive Success. Proceedings of the Royal Society B: Biological Sciences 279 (1748): 4845–4852.

Bates, D. M. Maechler, B. Bolker, and S. Walker. 2013. lme4: Linear Mixed-Effects Models Using Eigen and S4. http://CRAN.R-project.org/package=lme4.

Blaauw, B.R., and R. Isaacs. 2014. Flower Plantings Increase Wild Bee Abundance and the Pollination Services Provided to a Pollination-Dependent Crop. Journal of Applied Ecology.

Blüthgen, N., and A-M. Klein. 2011. Functional Complementarity and Specialisation: the Role of Biodiversity in Plant–Pollinator Interactions. Basic and Applied Ecology 12 (4): 282–291.

Brittain, C., C. Kremen, and A-M. Klein. 2013. Biodiversity Buffers Pollination from Changes in Environmental Conditions. Global Change Biology 19 (2): 540–547.

Brosi, B.J., G.C. Daily, T.M. Shih, F. Oviedo, and G. Durán. 2008. The Effects of Forest Fragmentation on Bee Communities in Tropical Countryside. Journal of Applied Ecology 45 (3): 773–783.

Button, L., and E. Elle. 2014. Wild Bumble Bees Reduce Pollination Deficits in a Crop Mostly Visited by Managed Honey Bees. Agriculture, Ecosystems & Environment 197: 255–263.

Carvalheiro, L.G., C.L. Seymour, S.W. Nicolson, and R. Veldtman. 2012. Creating Patches of Native Flowers Facilitates Crop Pollination in Large Agricultural Fields: mango as a Case Study. Journal of Applied Ecology 49 (6): 1373–1383.

Carvalheiro, L.G., R. Veldtman, A.G. Shenkute, G.B. Tesfay, C.W.W. Pirk, J. S. Donaldson, and S.W. Nicolson. 2011. Natural and Within-Farmland Biodiversity Enhances Crop Productivity. Ecology Letters 14 (3): 251–259.

Carvell, C., J.L. Osborne, A.F.G. Bourke, S.N. Freeman, R.F. Pywell, and M.S. Heard. 2011. Bumble Bee Species' Responses to a Targeted Conservation Measure Depend on Landscape Context and Habitat Quality. Ecological Applications 21 (5): 1760–1771.

Chagnon, M., J. Ingras, and D. de Oliveira. 1993. Complementary Aspects of Strawberry Pollination by Honey and Indigenous Bees (Hymenoptera). Journal of Economic Entomology 86 (2): 416–420.

Cilla, G., M. Caccavari, N.J. Bartoloni, and A. Roig-Alsina. 2012. The Foraging Preferences of Two Species of Melissodes Latreille (Hymenoptera, Apidae, Eucerini) in Farmed Sunflower in Argentina. Grana 51 (1): 63–75.

Decourtye, A., E. Mader, and N. Desneux. 2010. Landscape Enhancement of Floral Resources for Honey Bees in Agro-Ecosystems. Apidologie 41 (3): 264–277.

Ellis, J.D., J.D. Evans, and J. Pettis. 2010. Colony Losses, Managed Colony Population Decline, and Colony Collapse Disorder in the United States. Journal of Apicultural Research 49 (1): 134–136.

ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

Farm Service Agency-U.S. Department of Agriculture, 2006. Colusa County, 1-meter true color digital ortho photography, National Agriculture Imagery Program.

Free, J.B. 1964. The Behaviour of Honeybees on Sunflowers (Helianthus Annuus L.). Journal of Applied Ecology: 19–27.

Gallai, N., J-M. Salles, J. Settele, and B.E. Vaissiere. 2009. Economic Valuation of the Vulnerability of World Agriculture Confronted with Pollinator Decline. Ecological Economics 68 (3): 810–821.

Garibaldi, L.A., I. Steffan-Dewenter, R. Winfree, M.A. Aizen, R. Bommarco, S.A. Cunningham, C. Kremen, et al. 2013. Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. Science 339 (6127): 1608–1611.

Garibaldi, L.A., L.G. Carvalheiro, S.D. Leonhardt, M.A. Aizen, B.R. Blaauw, R. Isaacs, M. Kuhlmann, D. Kleijn, A-M. Klein, C. Kremen, L. Morandin, J. Scheper, and R.Winfree, 2014. From research to action: enhancing crop yield through wild pollinators. Frontiers in Ecology and the Environment 12:439–447.

Ghazoul, J. 2007. Recognising the Complexities of Ecosystem Management and the Ecosystem Service Concept. Gaia-Ecological Perspectives for Science and Society 16 (3): 215–221.

Gotelli, N.J., and R.K. Colwell. 2011. Estimating Species Richness. Biological Diversity: frontiers in Measurement and Assessment: 39–54.

Greenleaf, S.S., and C. Kremen. 2006. Wild Bees Enhance Honey Bees Pollination of Hybrid Sunflower. Proceedings of the National Academy of Sciences 103 (37): 13890–13895.

Greenleaf, S.S., N.M. Williams, R. Winfree, and C. Kremen. 2007. Bee Foraging Ranges and their Relationship to Body Size. Oecologia, 153(3): 589-596.

Hanes, S.P, K.K. Collum, A.K Hoshide, and E. Asare. 2013. Grower Perceptions of Native Pollinators and Pollination Strategies in the Lowbush Blueberry Industry. Renewable Agriculture and Food Systems: 1–8.

Hanley, M.E., M. Franco, C.E. Dean, E.L. Franklin, H.R. Harris, A.G. Haynes, S.R. Rapson, G. Rowse, K.C. Thomas, B.R. Waterhouse, and M.E. Knight. 2011. Increased bumblebee abundance along the margins of a mass flowering crop: evidence for pollinator spill-over. Oikos,120(11): 1618-1624.

Hannon, L.E., and T.T. Sisk. 2009. Hedgerows in an agri-natural landscape: potential habitat value for native bees. Biological conservation, 142(10): 2140-2154.

Hoehn, P., T. Tscharntke, J.M. Tylianakis, and I. Steffan-Dewenter. 2008. Functional Group Diversity of Bee Pollinators Increases Crop Yield. Proceedings of the Royal Society B: Biological Sciences 275 (1648): 2283–2291.

Holzschuh, A., C.F. Dormann, T. Tscharntke, and I. Steffan-Dewenter. 2011. Expansion of Mass-Flowering Crops Leads to Transient Pollinator Dilution and Reduced Wild Plant Pollination. Proceedings of the Royal Society B: Biological Sciences: rspb20110268.

Holzschuh, A., I. Steffan-Dewenter, and T. Tscharntke. 2008. Agricultural Landscapes with Organic Crops Support Higher Pollinator Diversity. Oikos 117 (3): 354–361.

Holzschuh, A., I. Steffan-Dewenter, D. Kleijn, and T. Tscharntke. 2007. Diversity of Flower-Visiting Bees in Cereal Fields: effects of Farming System, Landscape Composition and Regional Context. Journal of Applied Ecology 44 (1): 41–49.

Hurd, P.D., W.E. LeBerge, and E.G. Linsley. 1980. Principal Sunflower Bees of North America with Emphasis on the Southwestern United States (Hymenoptera, Apoidea)[Great Basin and Pacific Slope States]. Smithsonian Contributions to Zoology (USA).

Isaacs, R., and A.K. Kirk. 2010. Pollination Services Provided to Small and Large Highbush Blueberry Fields by Wild and Managed Bees. Journal of Applied Ecology 47 (4): 841–849.

Kevan, P.G., and T.P. Phillips. 2001. The Economic Impacts of Pollinator Declines: an Approach to Assessing the Consequences. Conservation Ecology 5 (1): 8.

Klein, A-M., C. Muller, P. Hoehn, and C. Kremen. 2009. Understanding the Role of Species Richness for Crop Pollination Services. Biodiversity, Ecosystem Functioning, and Human Wellbeing: 195–208.

Klein, A-M., B.E. Vaissiere, J.H. Cane, I. Steffan-Dewenter, S.A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of Pollinators in Changing Landscapes for World Crops. Proceedings of the Royal Society B: Biological Sciences 274 (1608): 303–313.

Kremen, C., N.M. Williams, and R.W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences 99(26): 16812-16816.

Kremen, C., K.S. Ullman, and R.W. Thorp. 2011. Evaluating the Quality of Citizen-Scientist Data on Pollinator Communities. Conservation Biology 25 (3): 607–617.

Kremen, C., and L.K. M'Gonigle. 2015. Small-scale restoration in intensive agricultural landscapes supports more specialized and less mobile pollinator species. Journal of Applied Ecology.

Kremen, C., and A. Miles. 2012. Ecosystem Services in Biologically Diversified Versus Conventional Farming Systems: benefits, Externalities, and Trade-Offs. Ecology and Society 17(4): 40.

Kremen, C., N.M. Williams, M.A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, et al. 2007. Pollination and Other Ecosystem Services Produced by Mobile Organisms: a Conceptual Framework for the Effects of Land-Use Change. Ecology Letters 10 (4): 299–314.

Kremen, C., N.M. Williams, and R.W. Thorp. 2002. Crop Pollination from Native Bees at Risk from Agricultural Intensification. Proceedings of the National Academy of Sciences 99 (26): 16812–16816.

Le Féon, V., F. Burel, R. Chifflet, M. Henry, A. Ricroch, B.E. Vaissière, and J. Baudry. 2013. Solitary Bee Abundance and Species Richness in Dynamic Agricultural Landscapes. Agriculture, Ecosystems & Environment 166: 94–101.

Long, R.F., A. Corbett, C. Lamb, C. Reberg-Horton, J. Chandler, and M. Stimmann. 1998. Beneficial insects move from flowering plants to nearby crops. California Agriculture 52(5): 23-26.

Long, R.F., J.L. Schmierer, D.J. Muier, K.M. Klonsky, and P. Livingston. 2011. Sample Costs to Produce Sunflowers for Seed Sacramento Valley. University of California Cooperative Extension, Agriculture and Natural Resources, Yolo County, CA.

Meffe, G.K. 1998. The Potential Consequences of Pollinator Declines on the Conservation of Biodiversity and Stability of Food Crop Yields. Conservation Biology 12 (1): 8–17.

Menz, M.H.M., R.D. Phillips, R. Winfree, C. Kremen, M.A. Aizen, S.D. Johnson, and K.W. Dixon. 2011. Reconnecting Plants and Pollinators: challenges in the Restoration of Pollination Mutualisms. Trends in Plant Science 16 (1): 4–12.

Morandin, L.A., and C. Kremen. 2013. Hedgerow Restoration Promotes Pollinator Populations and Exports Native Bees to Adjacent Fields. Ecological Applications 23 (4): 829–839.

Morandin, L.A., and M.L. Winston. 2006. Pollinators Provide Economic Incentive to Preserve Natural Land in Agroecosystems. Agriculture, Ecosystems & Environment 116 (3): 289–292.

Naidoo, R., A. Balmford, R. Costanza, B. Fisher, R.E. Green, B. Lehner, T.R. Malcolm, and T.H. Ricketts. 2008. Global Mapping of Ecosystem Services and Conservation Priorities. Proceedings of the National Academy of Sciences 105 (28): 9495–9500.

Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, M. Henry, H. Stevens, and H. Wagner. 2013. vegan: Community Ecology Package. http://CRAN.R-project.org/package=vegan.

Parker, F.D. 1981. Sunflower Pollination: abundance, Diversity, and Seasonality of Bees on Male-Sterile and Male-Fertile Cultivars. Environmental Entomology 10 (6): 1012–1017.

Pisanty, G., A-M. Klein, and Y. Mandelik. 2014. Do wild bees complement honeybee pollination of confection sunflowers in Israel? Apidologie 45(2): 235-247.

Potts, S.G., J.C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W.E. Kunin. 2010. Global Pollinator Declines: trends, Impacts and Drivers. Trends in Ecology & Evolution 25 (6): 345–353.

Rands, S.A., and H.M. Whitney. 2010. Effects of pollinator density-dependent preferences on field margin visitations in the midst of agricultural monocultures: A modelling approach. Ecological Modelling 221(9): 1310-1316.

Ricketts, T. H., J. Regetz, I. Steffan-Dewenter, S.A. Cunningham, C. Kremen, A. Bogdanski, A., B. Gemmill-Herren, S.S. Greenleaf, A-M. Klein, M.M. Mayfield, L.A. Morandin, A. Ochieng, and B.F. Viana. (2008). Landscape effects on crop pollination services: are there general patterns? Ecology letters, 11(5): 499-515.

Smith, K.M., E.H. Loh, M.K. Rostal, C.M. Zambrana-Torrelio, L. Mendiola, and P. Daszak. 2013. Pathogens, Pests, and Economics: Drivers of Honey Bee Colony Declines and Losses. EcoHealth 10 (4): 434–445.

Stanley, D.A., and J.C. Stout. 2014. Pollinator sharing between mass-flowering oilseed rape and co-flowering wild plants: implications for wild plant pollination. Plant ecology, 215(3): 315-325.

Steffan-Dewenter, I., and K. Leschke. 2003. Effects of Habitat Management on Vegetation and Above-Ground Nesting Bees and Wasps of Orchard Meadows in Central Europe. Biodiversity & Conservation 12 (9): 1953–1968.

Steffan-Dewenter, I., S.G. Potts, and L. Packer. 2005. Pollinator Diversity and Crop Pollination Services Are at Risk. Trends in Ecology & Evolution 20 (12): 651–652.

Tallis, H., P. Kareiva, M. Marvier, and A. Chang. 2008. An Ecosystem Services Framework to Support Both Practical Conservation and Economic Development. Proceedings of the National Academy of Sciences 105 (28): 9457–9464.

Tscharntke, T., A-M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape Perspectives on Agricultural Intensification and Biodiversity–Ecosystem Service Management. Ecology Letters 8 (8): 857–874.

Vaughan, M., and M. Skinner. 2008. Using Farm Bill Programs for Pollinator Conservation. USDANRCS National Plant Data Center, Online: http://www. Xerces. Org/Wp-Content/Uploads/2008/11/Using_Farm_Bill_Programs_Xerces_Society. Pdf.

Williams, Neal M, James Regetz, and Claire Kremen. 2012. "Landscape-Scale Resources Promote Colony Growth but Not Reproductive Performance of Bumble Bees." *Ecology* 93 (5): 1049–1058.

Winfree, R., N.M. Williams, J. Dushoff, and C. Kremen. 2007. Native Bees Provide Insurance Against Ongoing Honey Bee Losses. Ecology Letters 10: 1105–1113.

Winfree, R., B.J. Gross, and C. Kremen. 2011. Valuing Pollination Services to Agriculture. Ecological Economics 71: 80–88.

Zuur, A., E.N. Ieno, N. Walker, A.A. Saveliev, and G.M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer.

Web references

California Department of Pesticide Regulation, Pesticide Use Reporting. *Accessed October 5, 2014.* http://www.cdpr.ca.gov/docs/pur/purmain.htm

California Crop Improvement Association. *Accessed October 20, 2014.* http://ccia.ucdavis.edu/

Yolo Country Weights and Measures, Crop Statistics. *Accessed October 24, 2014.* http://www.yolocounty.org/general-government/general-government-departments/agriculture-cooperative-extension/agriculture-and-weights-measures/crop-statistics

Figures

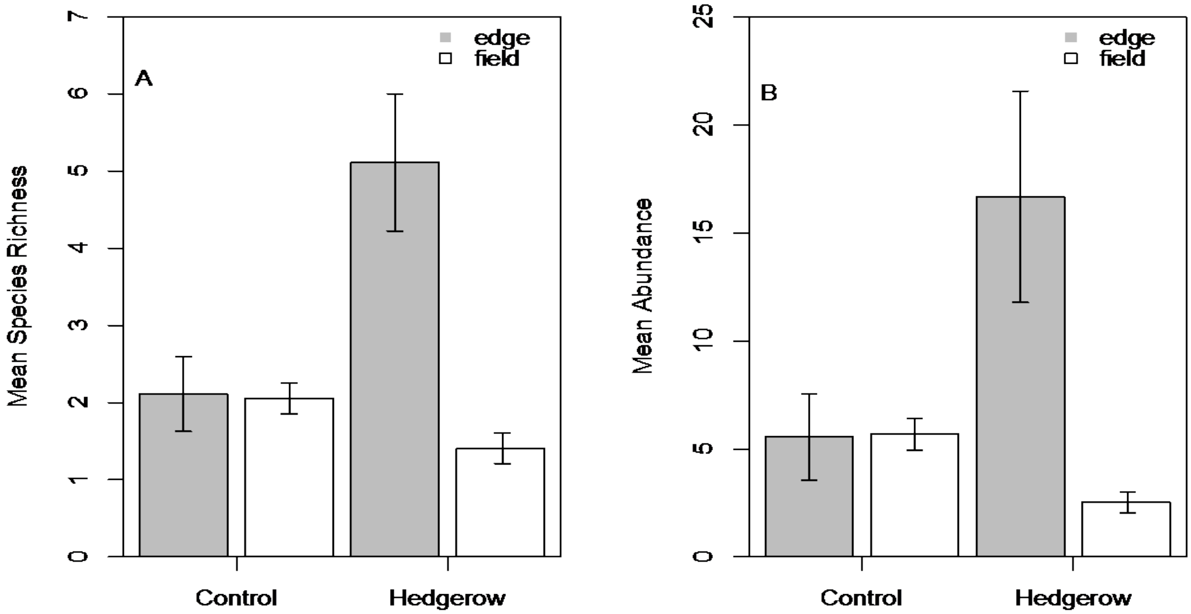


Figure 1. Hedgerow edges supported higher species richness (a) and abundance (b) of wild bees than control edges and sunflower fields.

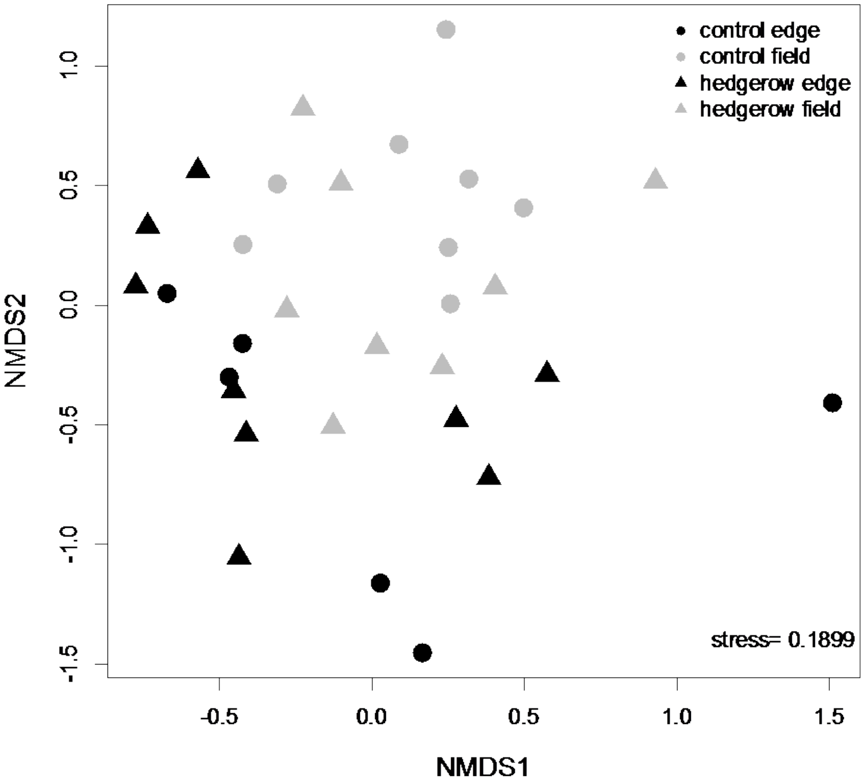


Figure 2. Chao1 (abundance-based) dissimilarities between wild bee communities found in control edges, hedgerows, control fields and hedgerow fields; visualized using non-metric dimensional scaling. All sites with fewer than one specimen were excluded from this perMANOVA analysis.

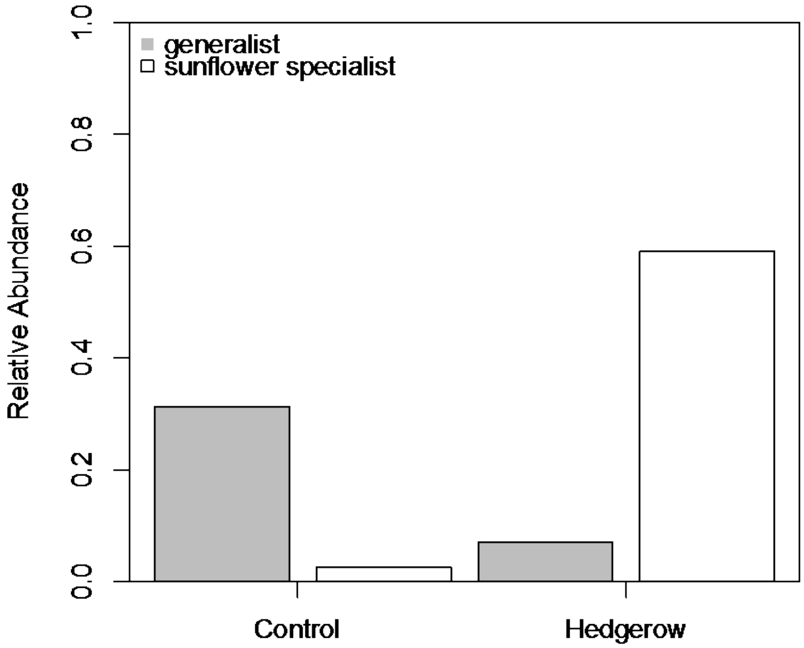


Fig 3. In the independent data set, more sunflower specialists were found in sites with hedgerows, indicating a significant interaction between hedgerow presence and wild bee specialization on sunflower.

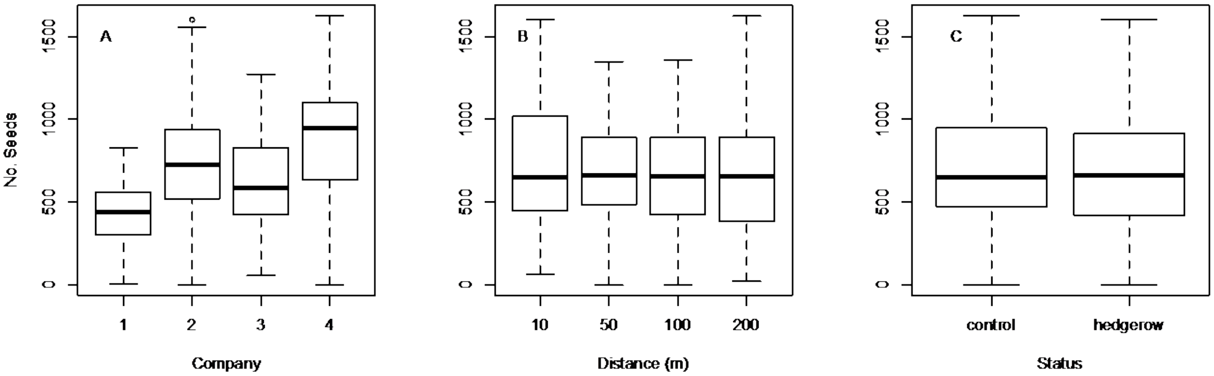
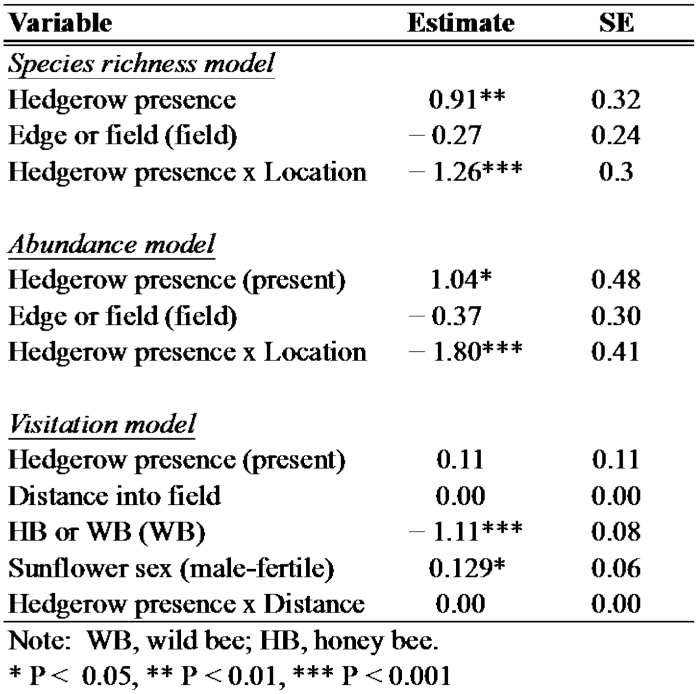


Figure 4. Sunflower variety, which was associated with seed company (a), strongly influenced rates of sunflower seed set. Neither distance from the edge (b) nor hedgerow presence (status; c) impacted seed set. The dark line in each box shows the mean, the outer lines of the box denotes the 1st (lower) and 3rd (upper) quartiles, and the whiskers show the minimum and maximum values.

Tables

Table 1. Model results for abundance and species richness of netted wild bees, and visitation of wild and honey bees, in sunflower fields adjacent to hedgerows or unenhanced in field edges..

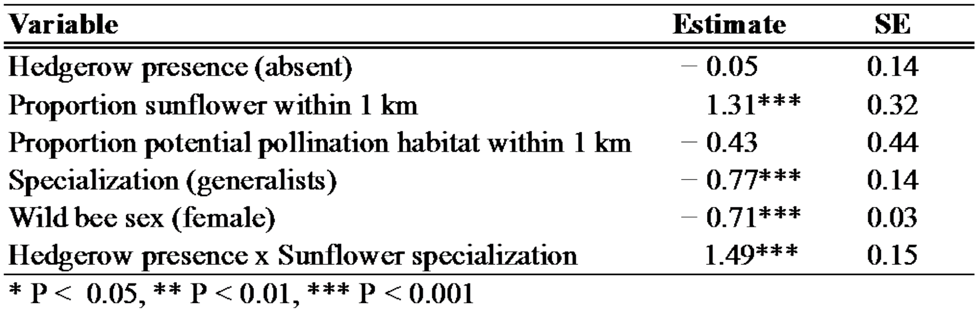


Variable	Estimate	SE
Species richness model		
Hedgerow presence	0.91**	0.32
Edge or field (field)	– 0.27	0.24
Hedgerow presence x Location	– 1.26***	0.3
Abundance model		
Hedgerow presence (present)	1.04*	0.48
Edge or field (field)	– 0.37	0.30
Hedgerow presence x Location	– 1.80***	0.41
Visitation model		
Hedgerow presence (present)	0.11	0.11
Distance into field	0.00	0.00
HB or WB (WB)	– 1.11***	0.08
Sunflower sex (male-fertile)	0.129*	0.06
Hedgerow presence x Distance	0.00	0.00

Note: WB, wild bee; HB, honey bee.

* P < 0.05, ** P < 0.01, *** P < 0.001

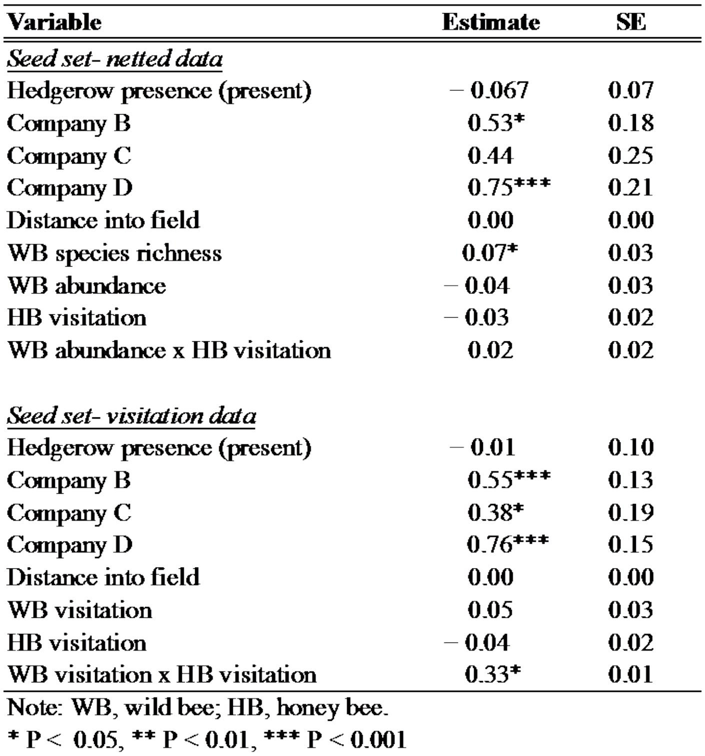
Table 2. Model results for the independent analysis assessing the use of field edges by sunflower specialists, categorized as primary oligoleges (Hurd 1980).



Variable	Estimate	SE
Hedgerow presence (absent)	– 0.05	0.14
Proportion sunflower within 1 km	1.31***	0.32
Proportion potential pollination habitat within 1 km	– 0.43	0.44
Specialization (generalists)	– 0.77***	0.14
Wild bee sex (female)	– 0.71***	0.03
Hedgerow presence x Sunflower specialization	1.49***	0.15

* P < 0.05, ** P < 0.01, *** P < 0.001

Table 3. Model results for netted and visitation models where sunflower seed set was the dependent variable. Site was nested within pair, which was included as a random factor in both models.



Variable	Estimate	SE
Seed set- netted data		
Hedgerow presence (present)	− 0.067	0.07
Company B	0.53*	0.18
Company C	0.44	0.25
Company D	0.75***	0.21
Distance into field	0.00	0.00
WB species richness	0.07*	0.03
WB abundance	− 0.04	0.03
HB visitation	− 0.03	0.02
WB abundance x HB visitation	0.02	0.02
Seed set- visitation data		
Hedgerow presence (present)	− 0.01	0.10
Company B	0.55***	0.13
Company C	0.38*	0.19
Company D	0.76***	0.15
Distance into field	0.00	0.00
WB visitation	0.05	0.03
HB visitation	− 0.04	0.02
WB visitation x HB visitation	0.33*	0.01

Note: WB, wild bee; HB, honey bee.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Appendix B: Supplement

Description of Independent Dataset

The independent dataset is part of a larger research program conducted by Dr. Claire Kremen in Yolo County, California. The goal of the study is to compare patterns of wild bee occupancy, persistence, abundance, and diversity in field edges with and without hedgerow enhancements (see Morandin and Kremen 2013; M’Gonigle et al., *in press*; Kremen and M’Gonigle 2015). Hedgerows are linear plantings of native woody shrubs and forbs that were planted to provide forage and habitat for beneficial insects, including both bees and natural enemies. Hedgerows take approximately 5 years for plants to mature, thus all hedgerows were planted at least 5 years and up to 12 years before our study. (Morandin and Kremen 2013). A total of 21 hedgerow sites and 24 controls that have been sampled over time, starting in 2006, with new sites added in 2012 to expand the scope of the study. Control sites were selected such that the adjacent crop types and landscape context were similar to their paired hedgerows sites. Control sites varied from bare edges to weedy edges, including some wooded or shrubby edges, to capture the range of edges present in the greater landscape. We limited our analyses of this dataset to the two years of our study, 2012 and 2013.

Sampling occurs in 4-5 rounds— from April through August— in order to capture wild bee diversity across seasons. Bees are netted for 1 hour, not including specimen handling, in each site during each sampling round. Only bees contacting reproductive parts of blooms are collected. Bees are only collected on clear days with wind speeds < 2.5 m/s and temperatures > 18°C. After collection, bees were pinned and then identified by Dr. Robbin Thorp, Professor Emeritus, University of California, Davis. All specimens are deposited in the collections of the Essig Museum of Invertebrate Zoology at the University of California, Berkeley.

Supplemental Figures

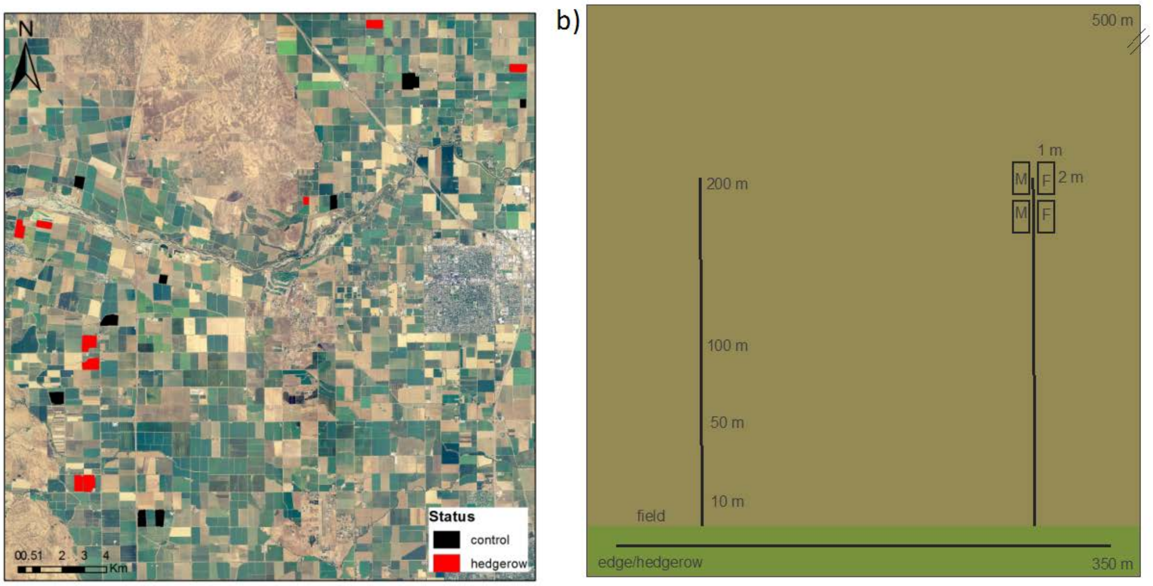


Fig. S1. Our study was conducted in 18 hybrid sunflower fields (9 controls and 9 hedgerows) in Yolo County, CA, a highly intensive agricultural region (a). We recorded bee visitation and netted bees on blooms in edges and in four 1 x 2 m plots on male-fertile (M) and male-sterile (F) plots at each distance (10, 50, 100 and 200 m) along two 200 m transects that were 100 m apart in each field (b). We also collected 3 sunflower heads at each distance along the field transects for seed set calculations.

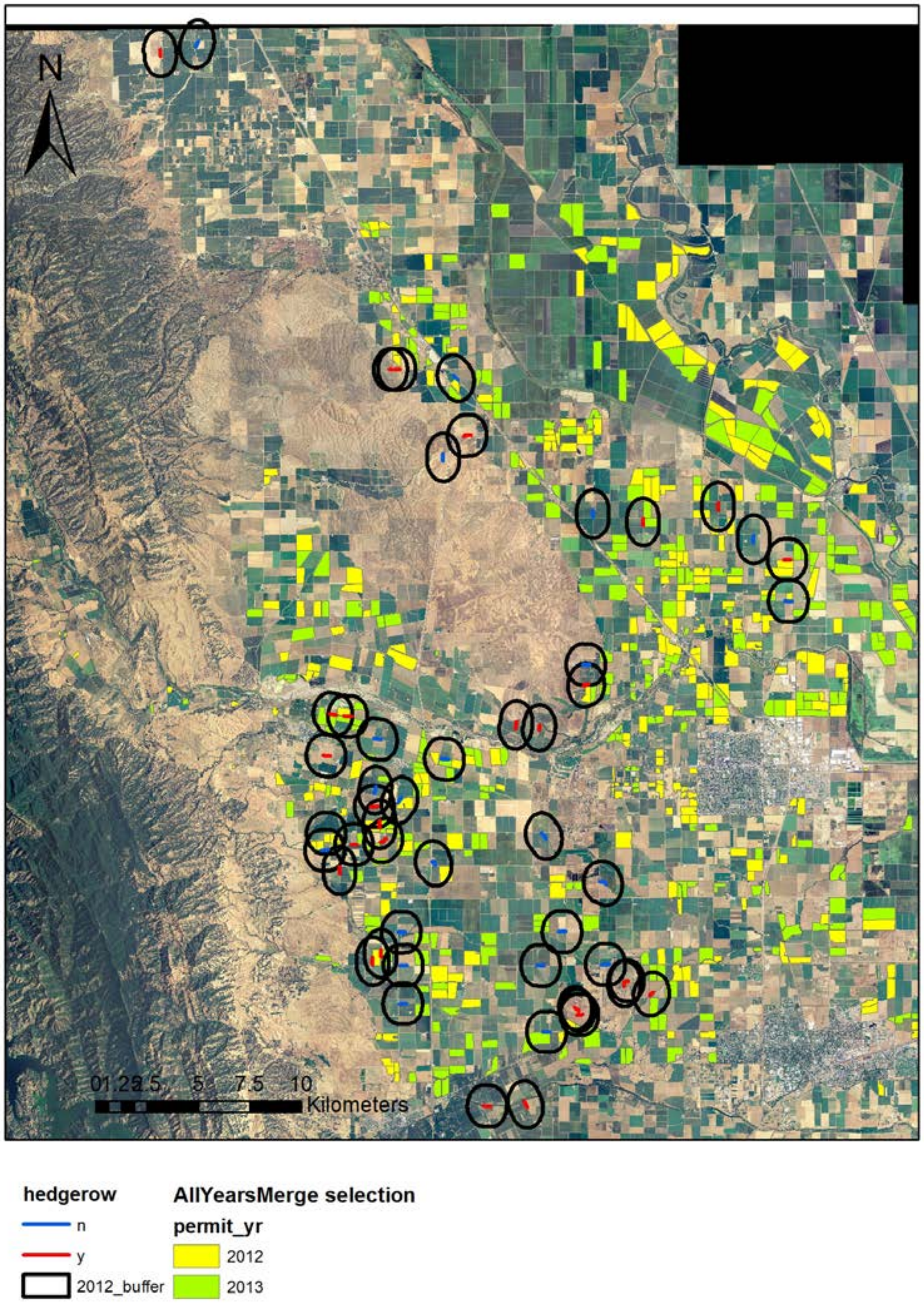


Fig. S2. Hedgerow and control edge sites from independent study in 2012- 13 (C. Kremen et al., *unpublished data*).

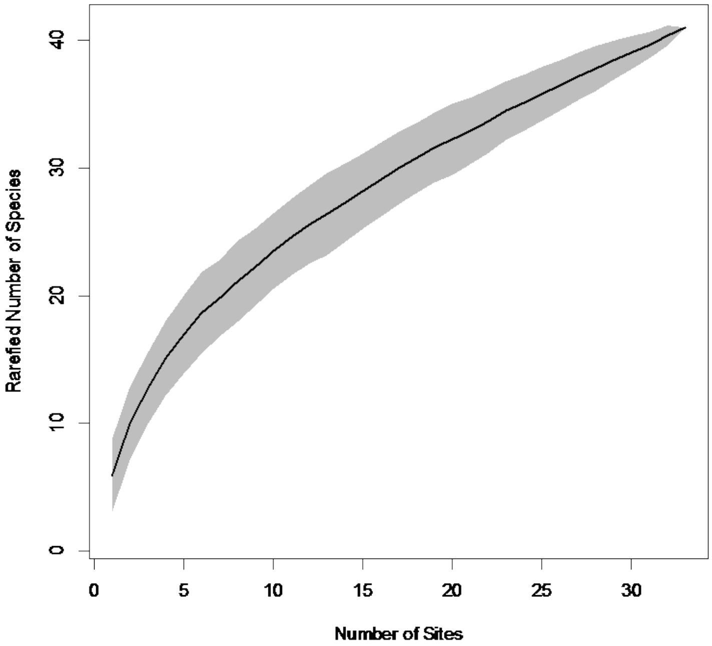


Fig. S3. Species accumulation curve; includes both control and hedgerow sites, field and edges.

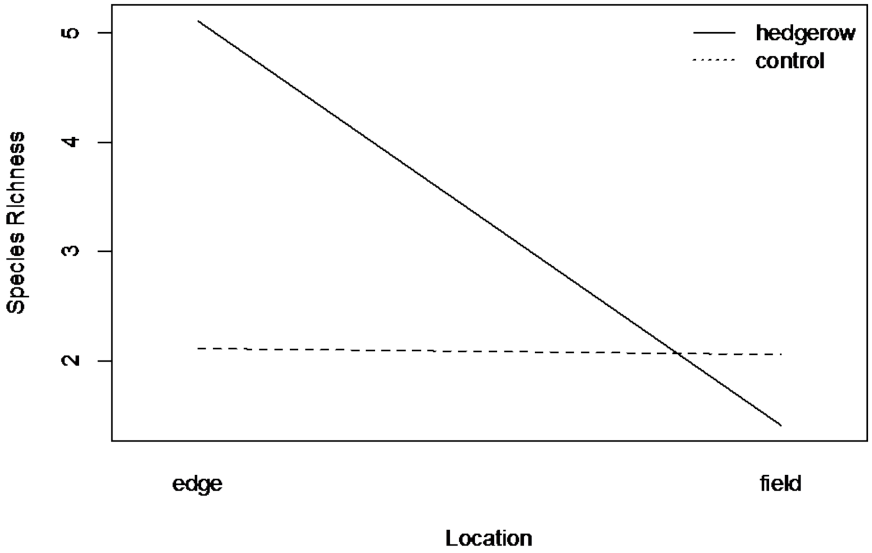


Fig. S4. Interaction plot of hedgerow presence with location (field or edge) on wild bee species richness. There is a significant interaction of hedgerow presence in edges, but not in fields.

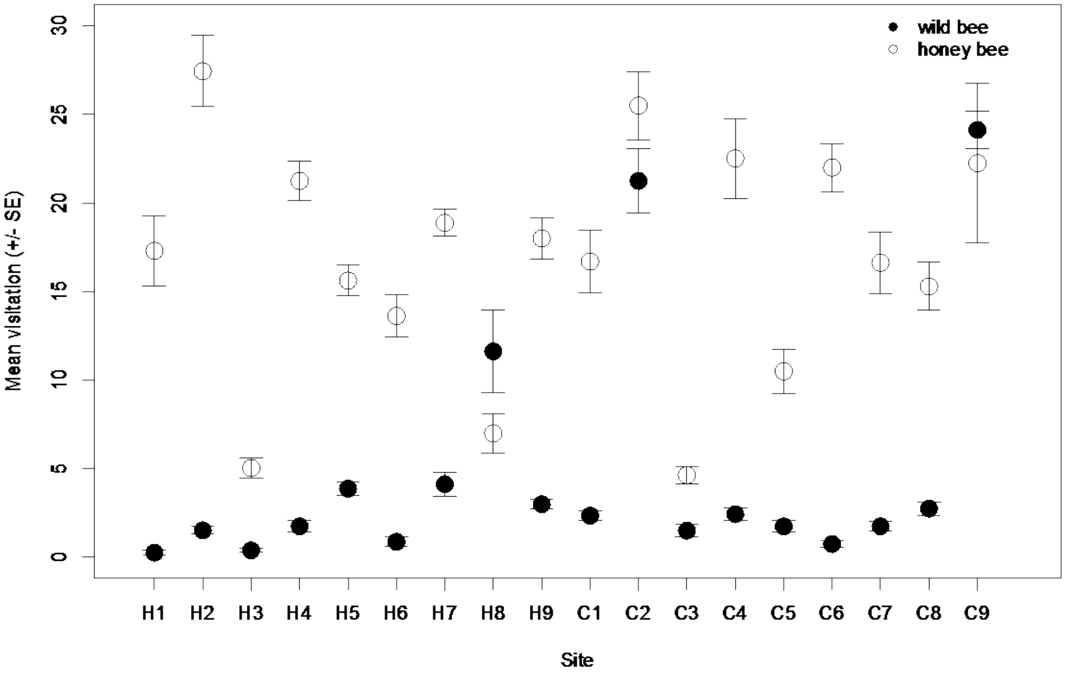


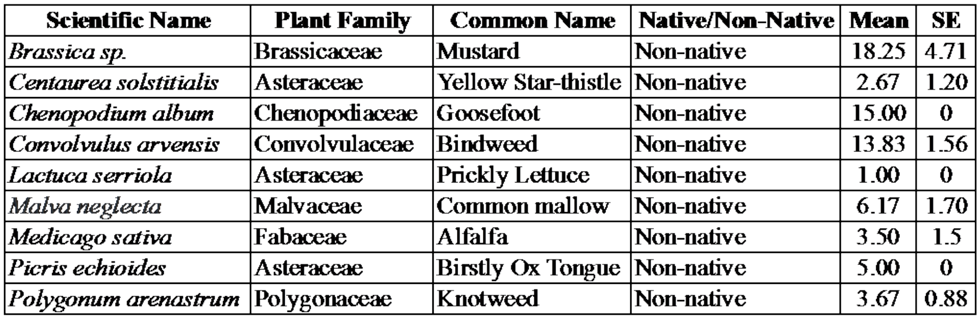
Fig. S5. Visitation rates (mean +/- SE) of honey bees and wild bees aggregated across both male-sterile and male-fertile sunflower heads observed during thirty-two 2 minutes sampling periods at each site.

Supplemental Tables

Table S1. Average (mean ± SE) percent bloom of plants flowering in hedgerow sites.

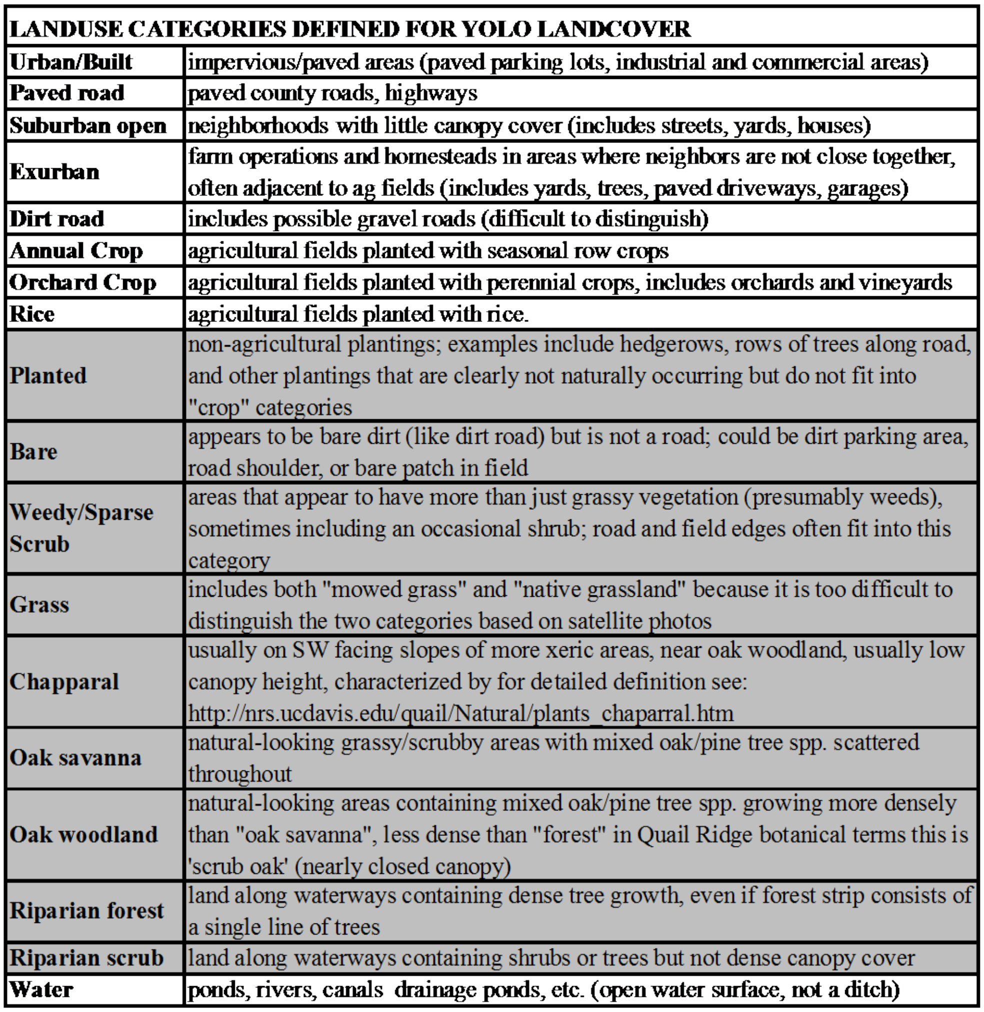
Scientific Name	Plant Family	Common Name	Native/Non-Native	Mean	SE
Ammi visnaga	Apiaceae	Toothpickweed	Non-native	2.00	0
Asclepia fascicularis	Apocynaceae	Narrowleaf Milkweed	Native	8.00	0
Atriplex triangularis	Chenopodiaceae	Saltbrush	Native	22.50	17.50
Brassica sp.	Brassicaceae	Mustard	Non-native	10.20	2.50
Centaurea solstitialis	Asteraceae	Yellow Star-thistle	Non-native	3.00	1.68
Convolvulus arvensis	Convolvulaceae	Bindweed	Non-native	8.83	1.26
Daucus carota	Apiaceae	Queen Anne's Lace	Non-native	17.33	6.36
Eriogonum fasciculatum	Polygonaceae	Buckwheat	Native	73.00	7.30
Foeniculum vulgare	Apiaceae	Fennel	Non-native	10.00	0
Grindelia camporum	Asteraceae	Gumplant	Native	18.00	0
Heteromeles arbutifolia	Rosaceae	Toyon	Native	21.86	8.46
Lactuca serriola	Asteraceae	Prickly Lettuce	Non-native	1.00	0
Lotus corniculatus	Fabaceae	Birdsfoot Trefoil	Non-native	19.00	0
Picris echioides	Asteraceae	Birstly Ox Tongue	Non-native	9.92	2.90
Rosa californica	Rosaceae	California Rose	Native	5.00	0
Sambucus mexicana	Adoxaceae	Elderberry	Native	11.00	2.25

Table S2. Average (mean ± SE) percent bloom of plants flowering in control sites.



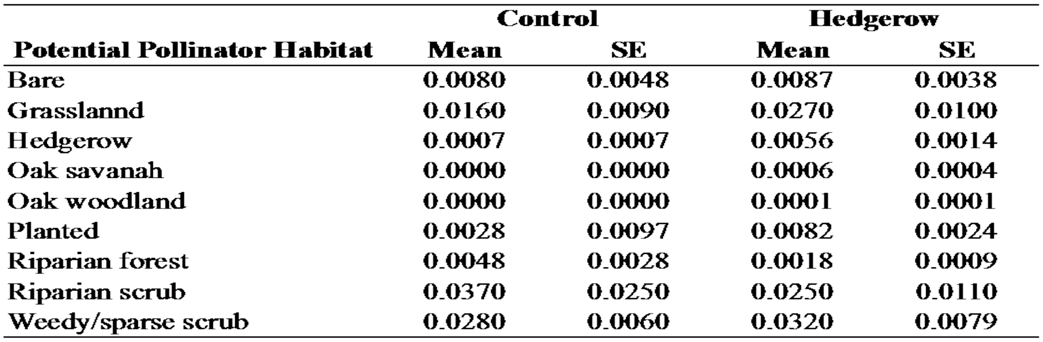
Scientific Name	Plant Family	Common Name	Native/Non-Native	Mean	SE
Brassica sp.	Brassicaceae	Mustard	Non-native	18.25	4.71
Centaurea solstitialis	Asteraceae	Yellow Star-thistle	Non-native	2.67	1.20
Chenopodium album	Chenopodiaceae	Goosefoot	Non-native	15.00	0
Convolvulus arvensis	Convolvulaceae	Bindweed	Non-native	13.83	1.56
Lactuca serriola	Asteraceae	Prickly Lettuce	Non-native	1.00	0
Malva neglecta	Malvaceae	Common mallow	Non-native	6.17	1.70
Medicago sativa	Fabaceae	Alfalfa	Non-native	3.50	1.5
Picris echioides	Asteraceae	Birstly Ox Tongue	Non-native	5.00	0
Polygonum arenastrum	Polygonaceae	Knotweed	Non-native	3.67	0.88

Table S3. Land use categories utilized to classify potential pollinator habitat (categories in grey) within a 1 km buffer around each site on aerial photographs of Yolo County, CA from the National Agriculture Imagery Program (NAIP). Categories were created in collaboration with K. Cutler, L.K. M'Gonigle, and L. Morandin.



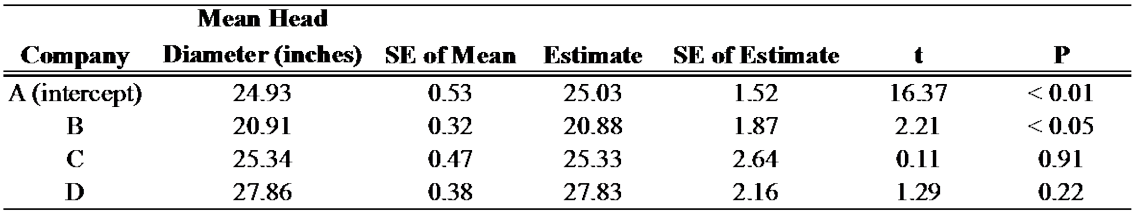
LANDUSE CATEGORIES DEFINED FOR YOLO LANDCOVER	
Urban/Built	impervious/paved areas (paved parking lots, industrial and commercial areas)
Paved road	paved county roads, highways
Suburban open	neighborhoods with little canopy cover (includes streets, yards, houses)
Exurban	farm operations and homesteads in areas where neighbors are not close together, often adjacent to ag fields (includes yards, trees, paved driveways, garages)
Dirt road	includes possible gravel roads (difficult to distinguish)
Annual Crop	agricultural fields planted with seasonal row crops
Orchard Crop	agricultural fields planted with perennial crops, includes orchards and vineyards
Rice	agricultural fields planted with rice.
Planted	non-agricultural plantings; examples include hedgerows, rows of trees along road, and other plantings that are clearly not naturally occurring but do not fit into "crop" categories
Bare	appears to be bare dirt (like dirt road) but is not a road; could be dirt parking area, road shoulder, or bare patch in field
Weedy/Sparse Scrub	areas that appear to have more than just grassy vegetation (presumably weeds), sometimes including an occasional shrub; road and field edges often fit into this category
Grass	includes both "mowed grass" and "native grassland" because it is too difficult to distinguish the two categories based on satellite photos
Chapparal	usually on SW facing slopes of more xeric areas, near oak woodland, usually low canopy height, characterized by for detailed definition see: http://nrs.ucdavis.edu/quail/Natural/plants_chaparral.htm
Oak savanna	natural-looking grassy/scrubby areas with mixed oak/pine tree spp. scattered throughout
Oak woodland	natural-looking areas containing mixed oak/pine tree spp. growing more densely than "oak savanna", less dense than "forest" in Quail Ridge botanical terms this is 'scrub oak' (nearly closed canopy)
Riparian forest	land along waterways containing dense tree growth, even if forest strip consists of a single line of trees
Riparian scrub	land along waterways containing shrubs or trees but not dense canopy cover
Water	ponds, rivers, canals drainage ponds, etc. (open water surface, not a ditch)

Table S4. Average proportion of potential pollinator habitat in a 1 km buffer around unenhanced and hedgerow field edges.



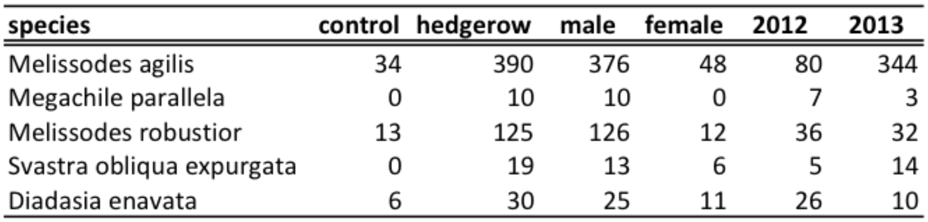
	Control		Hedgerow	
Potential Pollinator Habitat	**Mean**	**SE**	**Mean**	**SE**
Bare	0.0080	0.0048	0.0087	0.0038
Grasslannd	0.0160	0.0090	0.0270	0.0100
Hedgerow	0.0007	0.0007	0.0056	0.0014
Oak savanah	0.0000	0.0000	0.0006	0.0004
Oak woodland	0.0000	0.0000	0.0001	0.0001
Planted	0.0028	0.0097	0.0082	0.0024
Riparian forest	0.0048	0.0028	0.0018	0.0009
Riparian scrub	0.0370	0.0250	0.0250	0.0110
Weedy/sparse scrub	0.0280	0.0060	0.0320	0.0079

Table S5. Model results for the effect of company on sunflower head size.



Company	Mean Head Diameter (inches)	SE of Mean	Estimate	SE of Estimate	t	P
A (intercept)	24.93	0.53	25.03	1.52	16.37	< 0.01
B	20.91	0.32	20.88	1.87	2.21	< 0.05
C	25.34	0.47	25.33	2.64	0.11	0.91
D	27.86	0.38	27.83	2.16	1.29	0.22

Table S6. Male and female sunflower specialists found in control and hedgerows edges in 2012-13 (Kremen et al., *unpublished data*).



species	control	hedgerow	male	female	2012	2013
Melissodes agilis	34	390	376	48	80	344
Megachile parallela	0	10	10	0	7	3
Melissodes robustior	13	125	126	12	36	32
Svastra obliqua expurgata	0	19	13	6	5	14
Diadasia enavata	6	30	25	11	26	10

Table S7. Species collected in sunflower fields and field edges. We assigned specialization to sunflower based on Hurd's primary and secondary oligolege categorizations (1980). Visitation categories were adapted from the citizen science classifications from Kremen et al. (2011). Small carpenter bees were collapsed into the tiny dark bee category. BB- bumble bee; HBB- Hairy belly bee; HLB- Hairy legged bee; PB- parasitic bee; SSB- stripped sweat bee; TDB- tiny dark bee.

Species	Sunflower specialist	Visitation category	Size	Control edge	Hedgerow edge	Control field	Hedgerow field
Anthophora urbana		HLB	medium	0	1	2	1
Apis mellifera		HB	medium	NA	NA	NA	NA
Bombus californicus		BB	large	0	0	0	1
Bombus vosnesenskii		BB	large	0	0	0	1
Ceratina arizonensis		TDB	tiny	0	1	0	0
Ceratina dallatorreana		TDB	tiny	0	1	0	0
Diadasia enavata	primary	HLB	medium	0	0	8	35
Halictus ligatus		SSB	small	3	12	4	13
Halictus tripartitus		SSB	small	12	25	3	12
Hylaeus conspicuus		TDB	tiny	0	1	0	0
Hylaeus mesillae		TDB	tiny	0	3	0	0
Lasioglossum incompletum		TDB	tiny	11	9	7	6
Lasioglossum tegulariforme		TDB	tiny	4	4	6	2
Lasioglossum Dialictus sp. D		TDB	tiny	1	2	0	0
Lasioglossum Dialictus spp.		TDB	tiny	2	0	0	0
Megachile apicalis		HBB	medium	1	2	0	3
Megachile coquilletti		HBB	medium	0	1	0	0
Megachile gentilis		HBB	medium	0	3	1	0
Megachile montivags		HBB	medium	0	0	210	0
Melissodes agilis	primary	HLB	medium	0	0	71	50
Melissodes lupina	secondary	HLB	medium	0	9	16	24
Melissodes robustior	primary	HLB	medium	0	0	0	3
Melissodes stearnsi	secondary	HLB	medium	0	1	0	2
Sphecodes sp. B		PB	tiny	1	0	0	0
Sphecodes spp.		PB	tiny	2	0	0	0
Svastra obliqua expurgata	primary	HLB	large	0	0	45	7
Triepeolus concavus		PB	medium	0	2	0	1
Triepeolus heterurus		PB	medium	4	0	1	1
Triepeolus melanarius		PB	medium	1	0	0	1
Triepeolus subnitens		PB	medium	0	1	11	0
Xeromelecta californica		PB	medium	0	0	1	1

Table S8. Plant species in control and hedgerow edges visited by male and female sunflower specialists (Kremen et al., *unpublished data*).

Plant species	Diadasia enavata		Megachile parallela		Melissodes agilis		Melissodes robustior		Svastra obliqua expurgata	
	f	m	f	m	f	m	f	m	f	m
Achillea millefolium	0	0	0	0	0	1	0	0	0	0
Ammi visnaga	1	5	0	0	5	15	0	0	2	1
Anthemis cotula	0	0	0	0	0	1	0	0	0	0
Brassica sp.	0	1	0	0	1	15	2	4	0	0
Buddleja davidii	1	0	0	0	0	0	0	0	0	0
Ceanothus sp.	0	0	0	0	0	3	0	0	0	0
Centaurea solstitialis	4	7	0	0	0	1	0	0	1	0
Cirsium bulbosum	0	0	0	0	0	0	0	0	1	1
Convolvulus arvensis	1	0	0	0	3	14	0	1	0	0
Eriogonum fasciculatum	0	5	0	8	31	214	3	55	2	3
Grindela hirsutula	0	1	0	0	0	0	0	0	0	0
Heliotropium curassavicum	0	3	0	0	1	1	0	0	0	0
Lactuca serriola	0	0	0	0	0	15	0	7	0	0
Lavandula officinalis	0	0	0	0	6	95	7	59	0	8
Malva parviflora	2	0	0	0	0	0	0	0	0	0
Picris echioides	2	3	0	2	0	1	0	0	0	0
Silybum marianum	0	0	0	0	0	2	0	0	0	0

Although hedgerows did not influence yields in adjacent mass-flowering crop fields, they did support populations of specialist bees important for crop pollination. Hedgerows are clearly important for the conservation of wild bees in agricultural landscapes. Hedgerows largely focus on enhancing vegetative diversity otherwise lacking in intensively farmed areas, however, bees also require nest sites to complete their life cycle. Whether hedgerows can also increase wild bee nesting indicates their ability to support sustainable wild bee populations over time. Nesting rates, however, have traditionally been challenging to measure because finding nest locations are hard to locate. In the next chapter, I test whether emergence traps can sample bees at their nest sites.

Chapter 2

Evaluating nesting microhabitat for ground-nesting bees using emergence traps

Hillary S. Sardiñas and Claire Kremen

Published in
Basic and Applied Ecology
Volume 15, Issue 2, Pages 161-168
March 2014

Abstract

Nesting resources structure native bee communities and the availability of suitable nests may enhance population abundance and persistence. Nesting rates of ground-nesting bees have proven challenging to assess due to a lack of standardized methods. We quantified the abundance of ground-nesting native bees using emergence traps over a seven-month study period. We then compared specimens captured in emergence traps with pan- and net-collected specimens. We hypothesized that ground-nesting bees would be highly similar to bees found foraging within our study site. However, the species assemblage of ground-nesting bees collected from emergence traps was significantly dissimilar from the assemblages collected with aerial nets and pan traps, indicating different sampling methods target different components of the species assemblage. We then examined the importance of nesting resources found at each emergence trap on the abundance of ground-nesting bees collected from emergence traps. Quantification of potential nesting resources, such as percent bare soil, has been proposed as a proxy of nesting habitat for ground-nesting guilds. The most predictive nest-site characteristics, at the community-level, were sloped ground and soil compaction. Further, spatial distribution of nesting resources within the study landscape also affected nesting rates, although this varied by species. Bees occurred in 85% of emergence traps, with sampling date strongly affecting the number of bees collected. Emergence traps provide a useful method of sampling the ground-nesting native bee community and investigating nesting incidence.

Keywords: Apiformes; Community dissimilarity; Hymenoptera; Aerial Netting; Pan traps; Zero-altered model

Introduction

Wild, unmanaged pollinators are effective, often critical contributors to pollination services in natural and managed systems (Garibaldi et al. 2013; Klein et al., 2007). Of these, native bees are the most important pollinator group (Kearns, Inouye, & Waser, 2008). Interest in native bee conservation has risen in tandem with honey bee (*Apis mellifera* L.) decline (Winfree, 2010; Menz, Phillips, Winfree, Kremen, Aizen, et al., 2010), and with increasing evidence of native bee population declines and local extinctions (e.g. Cameron et al., 2011). Yet little is known about one of the primary contributors to native bee life-history, nesting resources. As central-place foragers, native bees return to the same nest site after foraging bouts; therefore nest location is a key determinant of the distribution of pollination services in a given landscape (Lonsdorf et al., 2009).

Direct assessments of native bee nesting have focused on twig- and cavity-nesting guilds that readily occupy trap nests (e.g. Williams & Kremen, 2007; Steffan-Dewenter & Schiele, 2008). These guilds comprise less than 15% of all bee species; Instead, the majority of native bees are solitary ground-nesters (Cane, 1991; Michener, 2007).

Ground-nesting bees can be assessed using tent traps that cover a portion of the ground, known as emergence traps (e-traps). E-traps have rarely been used to assess ground-nesting rates (e.g. Kim et al., 2006), they are more commonly utilized to assess emerging pests. Standard bee collection techniques are pan-traps (colored bowls filled with soapy water) and aerial netting at flowers (Westphal et al., 2008), but these methods do not directly capture bees from their nests. Therefore the ability of habitat to support nesting is often inferred from (1) the presence of bee species from specific nesting guilds (e.g. Morandin & Kremen, 2013), or (2) the presence of potential nesting resources (e.g. Potts et al., 2005; Grundel et al., 2010). The first inference assumes that bees found at a location must be nesting somewhere within a distance corresponding to their foraging range (Lonsdorf et al. 2009), which varies from 300 m for small-bodied bees (e.g. *Lasioglossum*) to 2000 m for larger bees (e.g. *Bombus*; Greenleaf et al., 2007). The second inference assumes that the availability of nesting resources affects the ability of native bees to nest in a given area.

Nesting resources have only recently emerged as factors potentially governing native bee community composition (Potts et al., 2005), persistence (Keitt, 2009), and response to disturbance (Williams et al., 2010); to date, floral resources have been the primary focus. Nests can be challenging to locate, therefore proxies are used as a means of quantifying potential nesting resources and habitat conditions within a landscape. Within-site characteristics, such as exposed bare ground (Potts et al., 2005), litter cover (Grundel et al., 2010), soil compaction (Wuellner, 1999), sloping ground (Burkle & Alarcon, 2011), and number of potential nesting cavities (cracks or holes in the ground; Potts et al., 2005), have been correlated to native bee community structure, but they have not been explicitly linked to within-site nesting incidence. Additionally, the distribution of nesting resources within a site may influence the distribution of within-site nesting, particularly if species have strong nesting preferences (Michener et al., 1958; Wcislo, 1996; Potts & Wilmer, 1997; Wuellner, 1999). Habitats may not be uniform in their ability to support populations of nesting bees (Grundel et al., 2010), however, models increasingly use nesting proxies and expert opinion regarding nesting suitability of land cover types to predict bee abundance in agricultural landscapes (Lonsdorf et al., 2009; Kennedy et al., 2013). To improve these models and enhance conservation efforts, it is critical to test the accuracy of nesting proxies.

We used e-traps to examine whether species found nesting in our study site were similar to those detected using pan traps and aerial netting. We then determined which nesting resource proxies were correlated with native ground-nesting bee incidence. We hypothesized that: (1) species collected in e-traps would be a subset of the community collected using other sampling methods, however we expected to detect more similarities between e-trap and netted specimens because netting indicates direct use of within-site floral resources whereas pan traps may attract bees from a wider area (Morandin & Kremen, 2013); (2) specific site characteristics would be associated with higher nesting incidence and bee abundance in e-traps; and (3) nesting habitat would be unevenly distributed throughout the study site, displaying spatial structuring, resulting in clustering of ground-nesting species utilizing those resources.

Materials and methods

Our study was conducted in mixed chaparral grey pine habitat in the Capay Valley in Yolo Co., California (see Appendix A: Fig. 1). We delineated a 1x1 m grid over an 40 x 120 m area and placed 40 e-traps (BugDorm, 1.2 m^2; see Appendix A: Fig. 2) in randomly selected grid cells. We deployed e-traps continuously for the study duration, from May - October 2011. E-traps were staked down and edges secured with rebar to prevent bees from entering or exiting. Each e-trap contained a kill jar at its apex filled with 70% ethanol, which was changed approximately every 12 days, for a total of 11 sampling rounds. On days when e-trap kill jars were changed, we set out 24 pan traps (alternating blue, white and yellow) along 4 parallel 120 m transects for 4 hours starting at 09:00 (see Appendix Fig. 3). Immediately following pan trap set-up, we netted all bee species visiting flowers within the study area for 40 minutes using variable transect walks (Westphal et al., 2008). We stopped the clock during specimen handling and between floral patches; netting usually lasted 1-1.5 hours, from 09:30-11:00. Pan and net sampling was conducted on days with clear skies, temperatures above 18°C, and wind speeds below 2.5 m/s (Morandin & Kremen, 2013). We quantified nesting proxies (Table 1) in each e-trap following Potts et al. (2005) in May.

Statistical Methods

We characterized species richness of the entire community and for each collection method using a Chao1 (abundance-based) estimator of richness which corrects for undetected species (Chao et al., 2004) from the R package vegan (Oksanen et al., 2012; R core development team 2012). We compared Bray-Curtis, Chao and Jaccard dissimilarities between species assemblages of ground-nesting bees and parasites of ground-nesters collected by different sampling methods. First we calculated pairwise dissimilarities of the assemblages collected by each sampling method over the entire study period. Then, using perMANOVAs (Oksanen et al., 2012), which calculate dissimilarities between all sampling methods simultaneously, we assessed differences in species collected with each method for every sampling date, after removing all sampling date-method combinations in which fewer than 5 specimens were collected. We visualized the dissimilarities between methods using non-metric multidimensional scaling (NMDS). We then calculated the sample coverage of each sampling method by dividing the number of species collected by each method by the total number of species collected over the course of our study (Westphal et al., 2008).

The nesting data includes many e-trap samples with no bees (see Appendix A: Fig. 4); therefore to test our second hypothesis (specific resources are associated with bee nesting) we used a zero-altered model developed to deal with high number of zeros typical of count data. Zero-altered models contain two parts: a zero-altered model that models the binomial probability of observing a zero, and a count model that models the non-zero observations (Zuur et al., 2009). We first tested whether a Poisson or negative binomial distribution would better fit our data. Both the likelihood ratio test ($\chi^2 = 118.86$, $P = < 0.001$) and AIC scores (Poisson model 750.6624, negative binomial model 633.8002) indicated that a negative binomial distribution was more appropriate for our data, suggesting a degree of overdispersion. We therefore modeled bee abundance in e-traps over the entire study period using a zero-altered negative binomial model using the R package pscl (Zeileis et al., 2008).

We assessed nesting proxies by first removing any variables that were significantly correlated (see Appendix A: Table 1), after visually assessing the results of a Principle Components Analysis to confirm that correlated variables fell along similar major axes. Within an e-trap, slope categories summed to 100%, therefore this classification led to strong negative correlations between the slope covariates ($\varrho = -0.968$). Since slopes 30-60° and >60° fell along the opposite major axis from slope <30°, which also included the nesting proxy pre-existing cavities, we used only Slope <30° as a predictor in our model.

We centered the variables included in the count model (mean subtracted from value) to facilitate interpretation. We hypothesized that two factors contributed to the number of zeros observed in our data: sampling date, which affects bee seasonality (Morandin & Kremen, 2013), and e-trap location, which was randomly placed in a single grid cell over the study period, possibly missing adjacent bee nests. Therefore these variables were included in the zero-altered portion of the model. We simplified the model by dropping terms from both the count and zero-altered portions of the model following the protocol in Zuur et al. (2009). The final model contained all reduced candidate nesting proxy covariates (percent bare ground, percent cracks, number of pre-existing cavities, slope, soil surface compaction, and percent vegetation) in the count model, but only sampling date in the zero-altered portion of the model. We assessed the variance inflation factors (VIF) of nesting proxies included in the model to ensure they were not collinear. All VIF were below 3.0 (Zuur et al., 2007), indicating that reduction of correlated variables eliminated collinearity between model covariates.

Next, we examined whether nesting incidence (presence-absence) or abundance of the entire community of nesting bees collected in e-traps could be explained by the spatial pattern of nest location or was correlated to the distribution of nesting resources within the site, using multiple regression on Bray-Curtis distance matrices (Lichstein, 2006; Mandelik et al., 2012), which is an extension of the Mantel test in the R package ecodist (Goslee & Urban, 2007). We repeated this test for the genus *Lasioglossum*, which was the most commonly collected genus in e-traps, and also for individual species with incidence > 5% of all samples.

Results

Eighty-five percent of e-traps collected bees over the duration of our study. Estimating species accumulation by rarefaction indicated that the detection of new species had begun to level out over our 7 month study period (Fig. 1). Our study site had an observed species richness across all sample techniques of 54 species, with a Chao1 species richness estimate of 61.5 ± 6.2 (mean ± SE). Pan traps had the highest sample coverage, collecting 452 individuals from 35 species (Chao1 = 40 ± 12.724); netting produced 97 individuals from 26 species (Chao1 = 71.333 ± 62.534). E-traps collected 252 ground-nesting bees (164 females and 88 males) representing 15 species (Chao1 = 15.333 ± 1.870; see Appendix A: Table 2). The majority (97%) of bees in e-traps were small-bodied Halictidae, predominantly from the *Lasioglossum* and *Halictus* genera. Conversely, species collected in pan and net samples had a wider range of body sizes (from large-bodied *Bombus* to tiny *Perdita*).

The ground-nesting species assemblages and their parasites collected by pans, netting and e-traps were all significantly dissimilar from one another (Bray-Curtis: F = 4.8566, P = 0.001; Chao: F = 4.4113, P = 0.001; Jaccard: F = 3.7945, P = 0.001; Fig. 2). Overall, there was little overlap between species collected by different methods (Bray-Curtis pairwise dissimilarity pan-net: 0.8353, pan-e-trap: 0.8148, net-e-trap: 0.7492; Fig. 3). Further, the numbers of species collected by different sampling methods varied by season (Fig. 4.; see Appendix A: Table 2).

Slopes < 30° (-0.0912 ± 0.0371, estimate ± SE, P = 0.0141), surface soil compaction (-2.9324 ± 1.2417, P = 0.0182), and pre-existing holes (-0.2170 ± 0.0880, P = 0.0137) were negatively associated with native bee nesting abundance, whereas percent bare ground was slightly positively associated with nesting (0.0281 ± 0.0167, P = 0.0925), although only marginally significant. Sampling date strongly influenced the number of zeros we observed, with fewer zeros earlier in the year (May–June).

We did not detect spatial patterns in nesting incidence or abundance for the ground-nesting community or the genus *Lasioglossum* in relation to nest location or nesting resources (Table 2). Variability of sloped ground among e-traps significantly affected the abundance of some nesting *Lasioglossum* species (Table 2).

Discussion

Direct assessments of native bee nesting at the community-level are scarce due to a lack of standardized methods. As we here demonstrate, e-traps are a viable method for quantifying native bee nesting rates and associating ground-nesting species with specific nesting resources. E-traps had a high collection rate over the study duration and within each sample period, despite numerous instances in which no ground-nesting bee was found. Furthermore, e-traps had a low estimated number of unseen species particularly when compared to estimates of unseen species from pan and net samples. We found eight species in e-traps that were never captured in either pan or net surveys, indicating further that the method may complement existing bee surveying techniques (Fig. 3).

Contrary to our hypothesis, e-traps collected markedly different species than pan and net samples. The high levels of dissimilarity we observed in species assemblages collected using different sampling methods could be attributable to biases associated with these methods or differences in sampling effort related to how the methods are implemented.

It is challenging to compare sampling effort across different methods. Pan traps are a passive method whose effectiveness varies given the abundance of adjacent floral resources (e.g. Morandin & Kremen 2013). We collected higher numbers of species in pan traps towards the end of our study period (Fig. 4), which coincided with a sharp decline in floral resources. Conversely, the efficacy of aerial netting may benefit from presence of floral resources, but can vary with collector skill (Westphal et al., 2008). Our study area had low floral species richness, and we only found bees foraging on 5 of the 11 plant species in bloom over the course of the study (see Appendix A: Table 3). Trap nests, a passive collection method that measure nesting rates, of twig- and cavity-nesting bees, have low sample coverage when compared to pan and net. E-traps are a passive method that also quantify nesting rates, however in our study, e-traps had nearly twice the sample coverage Westphal et al. (2008) found trap nests to have (e-trap = 27.8%, trap nests = 14%).

Other factors may have contributed to the levels of dissimilarity we observed between collection methods. For example, the unique species collected in the e-traps may have been the only individuals present in our study landscape, preventing them from being collected by other sampling methods. E-traps covered only a fraction of the study landscape (<1%), therefore it would be surprising if they collected all the individuals of a species in our study locale. Alternately, bees found foraging and flying in our study site could have come from surrounding areas. Our study area was smaller than the predicted foraging ranges of the species collected, however, even if it encompassed foraging ranges, species nesting outside the study area could still visit the study area if their nests were adjacent. Finally, e-traps were set out for the duration of our study, therefore bees collected in e-traps were those emerging from nests initiated the year prior to our study. The assemblage of species in the e-traps may have better matched community composition in the previous year, contributing to the high levels of dissimilarity between sampling methods we observed. Because we did not sample the year before we conducted our study, we cannot test this prediction nor disentangle it from biases associated with other sampling methods. Previous research has shown that bee communities can be highly variable between years, experiencing high rates of species turnover (Williams et al., 2001; Petanidou et al., 2008). To eliminate this temporal issue in future studies we suggest collecting data on the flying community in the prior year to e-trap sampling or moving e-traps during the study period. With the latter method male bees would then need to be excluded from analyses as they may not represent ground-nest bees emerging from nests but may instead be resting in vegetation (Kim et al., 2006).

Our study is the first to confirm directly the importance of the availability and distribution of ground nesting resources for native bee ground-nesting incidence at the community level. In our study, surface soil compaction decreased the number of nesting bees within e-traps. Ground-nesting bees have a wide range of documented tolerances for soil compaction, tending toward softer soils, however their preferences can change depending on factors including adjacent nest density (Potts & Willmer, 1997).

Many species of ground-nesting bees display a wide range of nesting preferences (e.g. Potts & Wilmer, 1997). It may therefore be challenging to identify specific nesting characteristics influencing nesting incidence on a species by species basis. Indeed, Grundel et al. (2010) found that differences in nesting resources across a range of sites influenced the community composition of bees present within those sites. Similarly, the importance of nesting resources may vary with community composition. Variability both within and among sites may be key to promoting diverse bee communities. Although our study occurred in a single site, we found that the distribution of nesting resources influenced nesting incidence of some species. For example, steeper slopes were not evenly distributed in our study area, thus bees preferring sloped ground displayed evidence of spatial clustering.

The inter-correlation we detected between existing nesting proxies suggests that ongoing assessment of nesting resources is warranted. For example, following Potts et al. (2005), we created categories for variables such as slope. It might be more meaningful to use continuous rather than discrete measurements to facilitate estimation of the degree of sloped ground that best supports bee nesting. Additionally, nesting resources may not be stable over time. We quantified nesting resources once during our study period; to link resources available to different bees more accurately, it may be necessary to repeat assessments over each distinct flight period.

Despite the limitations of our sampling procedures, our results show that e-traps can be used to directly associate native bee ground-nesting to within-site nesting resources. E-traps can be used over a wide range of habitat types to evaluate the ability of existing nesting proxies to predict within site nesting. E-traps can help illuminate spatial patterns of nesting and highlight discrepancies between the species utilizing within-site floral resources versus those nesting and reproducing at the site. Further, e-traps may be able to help address key questions in bee biology, including whether the spatial distribution of nesting resources limits native bee nesting. These kinds of direct, rather than correlative, studies are necessary to assist in conserving and promoting ground-nesting bee populations in natural and managed landscapes.

References

Burkle, L. A., & Alarcon, R. (2011). The future of plant-pollinator diversity: Understanding interaction networks across time, space, and global change. *American Journal of Botany*, *98*, 528–538.

Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., et al. (2011). Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences*, *108*, 662–227.

Cane, J. H. (1991). Soils of Ground-Nesting Bees (Hymenoptera: Apoidea): Texture, Moisture, Cell Depth and Climate. *Journal of the Kansas Entomological Society*, *64*, 406–413.

Chao, A., Chazdon, R. L., Colwell, R. K., & Shen, T.-J. (2004). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, *8*, 148–159.

Garibaldi, L., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., et al. (2013). Wild pollinators enhance fruit set regardless of honey bee abundance. *Science, 339,* 1608–1611.

Goslee, S. C., & Urban, D. L. (2007). The ecodist Package for Dissimilarity-based Analysis of Ecological Data. *Journal of Statiscial Software*, *22*, 1–19.

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

Grundel, R., Frohnapple, K. J., Glowacki, G. A., Scott, P. E., & Pavlovic, N. B. (2010). Floral and nesting resources, habitat structure, and fire influence bee distribution across and open-forst gradient. *Ecological Applications*, *20*, 1678–1692.

Kearns, C. A., Inouye, D.W., & Waser, N. M. (1998). Endangered mutualisms: the conservation of plant–pollinator interactions. *Annual Review of Ecology and Systematics, 29*, 83–112.

Keitt, T. H. (2009). Habitat conversion, extinction thresholds, and pollination services in agroecosystems. *Ecological Applications*, *19*, 1561–1573.

Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., et al. (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems (M. Anderson, Ed.). *Ecology Letters*, *16,* 584–599.

Kim, J., Williams, N.M., & Kremen, C. (2006). Effects of cultivation and proximity to natural habitat on ground-nesting native bees in California sunflower fields. *Journal of the Kansas Entomological Society, 79*, 309–320.

Klein, A. M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., et al. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 303–313.

Lichstein, J. W. (2006). Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecology*, *188*, 117–131.

Lonsdorf, E., Kremen, C., Ricketts, T., Winfree, R., Williams, N., et al. (2009). Modelling pollination services across agricultural landscapes. *Annals of Botany*, *103*, 1589–1600.

Mandelik, Y., Winfree, R., Neeson, T., & Kremen, C. (2012). Complementary habitat use by wild bees in agro-natural landscapes. *Ecological Applications*, *25*, 1535–1546.

Menz, M. H. M., Phillips, R. D., Winfree, R., Kremen, C., Aizen, M. A., et al. (2010). Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. *Trends in Plant Science*, 1–9.

Michener, C. D. (2007). *Bees of the World 2nd Edition*. Johns Hopkins University Press.

Michener, C. D., Lange, R. B., Bigarella, J. J., & Salamuni, R. (1958). Factors Influencing the Distribution of Bees' Nests in Earth Banks. *Ecology*, *39*, 207–217.

Morandin, L.A., & Kremen, C. (2013). Hedgerow Restoration Promotes Pollinator Populations and Exports Native Bees to Adjacent Fields. *Ecological Applications, 23,* 829-839.

Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., Minchin, P. R., et al. (2012). Vegan: Community Ecology Package. *R package version 2.0-5*, 1–17.

Petanidou, T., Kallimanis, A. S., Tzanopoulos, J., Sgardelis, S. P., & Pantis, J. D. (2008). Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecology Letters*, *11*, 564–575.

Potts, S. G., & Willmer, P. (1997). Abiotic and biotic factors influencing nest-site selection by Halictus rubicundus, a ground-nesting halictine bee. *Ecological Entomology*, *23*, 319–328.

Potts, S. G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., et al. (2005). Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology*, *30*, 78–85.

Steffan-Dewenter, I., & Schiele, S. (2008). Do resources or natural enemies drive bee population dynamics in fragmented habitats? *Ecology*, *89*, 1375–1387.

Wcislo, W. T. (1996). Parasitism Rates in Relation to Nest Site in Bees and Wasps (Hymenoptera: Apoidea). *Journal of Insect Behavior*, *9*, 1–14.

Westphal, C., R. Bommarco, G. Carré, E. Lamborn, N. Morrison, et al. (2008). Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs*, *78,* 653–671.

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

Williams, N. M., Crone, E. E., Roulston, T. H., Minckley, R. L., Packer, L., et al. (2010). Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, *143*, 2280–2291.

Williams, N. M., Minckley, R. L., & Silveira, F. A. (2001). Variation in Native Bee Faunas and its Implications for Detecting Community Changes. *Ecology and Society*, 1–15.

Winfree, R. (2010). The conservation and restoration of wild bees. *Annals of the New York Academy of Sciences*, *1195*, 169–197.

Wuellner, C. T. (1999). Nest site preference and success in a gregarious ground-nesting bee Dieunomia trangulifera. *Ecological Entomology*, *24*, 471–479.

Zeileis, A., Kleiber, C., & Jackman, S. (2008). Regression Models for Count Data in R. *Journal of Statiscial Software*, *27*, 1–25.

Zuur, A. F., Ieno, E. N., & Smith, G. M. (2007). *Analyzing Ecological Data*. New York, NY: Springer New York.

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer New York.

Figures

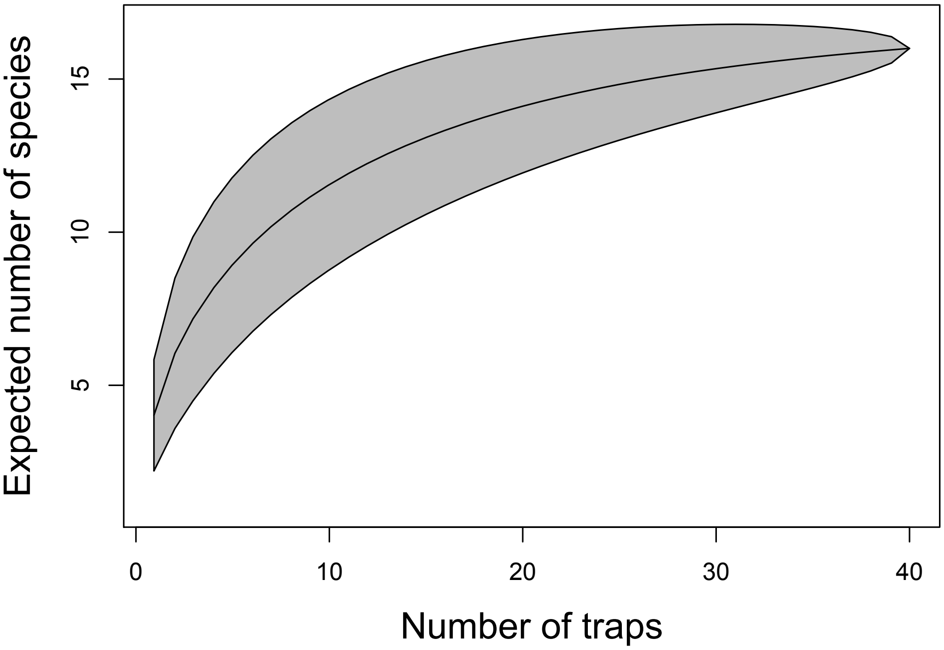


Fig. 1. Rarefaction by the number of traps shows that the number of species begins to saturate at a high number of traps. These data represent the number of species accumulated across the 7-month sample period in each trap. Shaded areas are 95% confidence intervals.

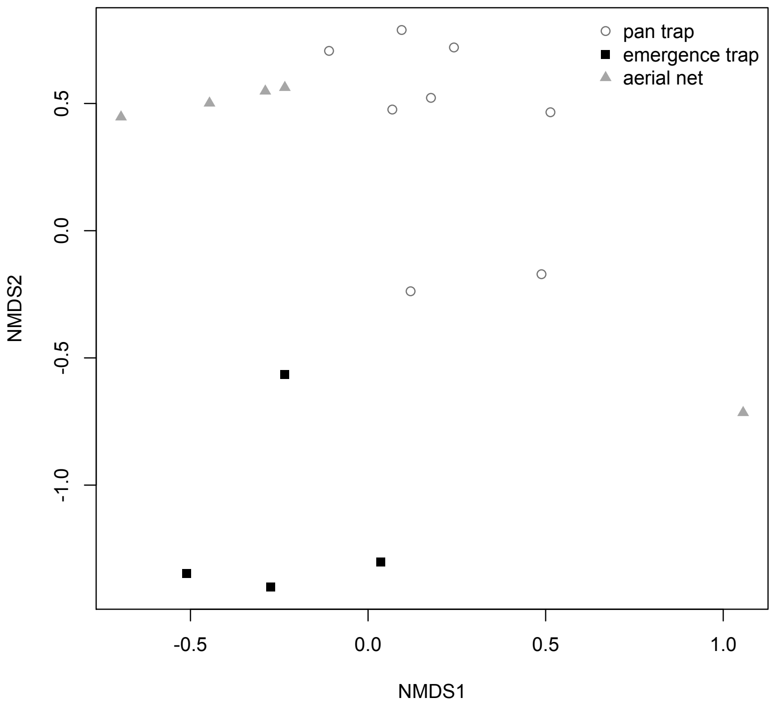


Fig. 2. NMDS plot of Bray-Curtis dissimilarities of species assemblages collected by pan trapping, aerial netting and emergence traps during 11 sampling events during the study period (NMDS, Stress = 0.10501). Samples with fewer than 5 individuals were removed from analysis.

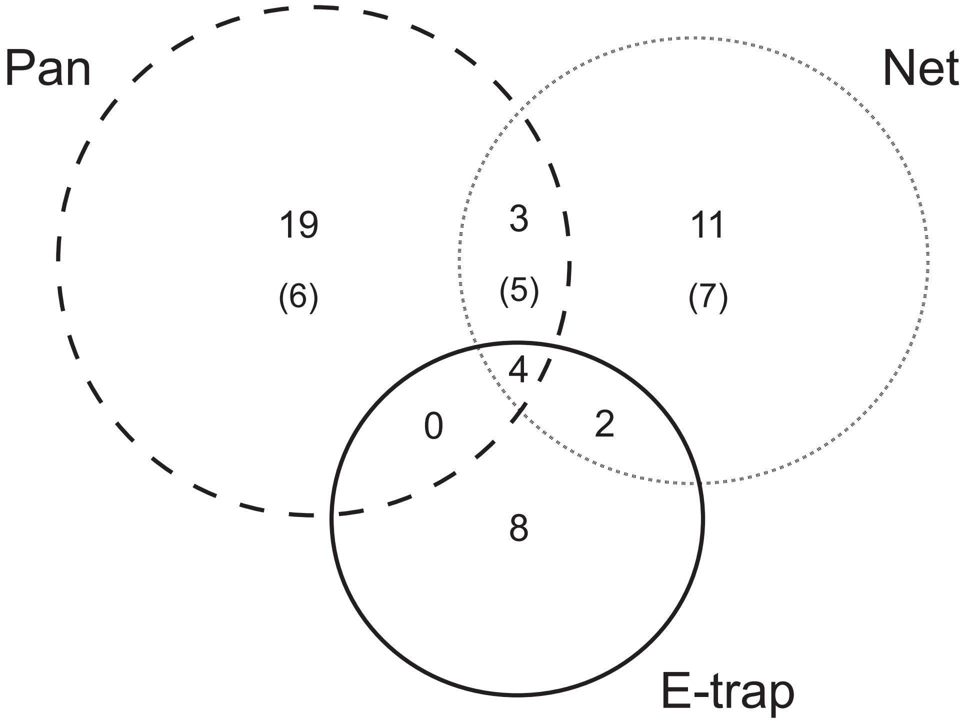


Fig. 3. Shared species collected by pan trapping, aerial netting and emergence traps. Number in parentheses indicate above-ground nesting species whereas all other numbers refer to below-ground nesting species.

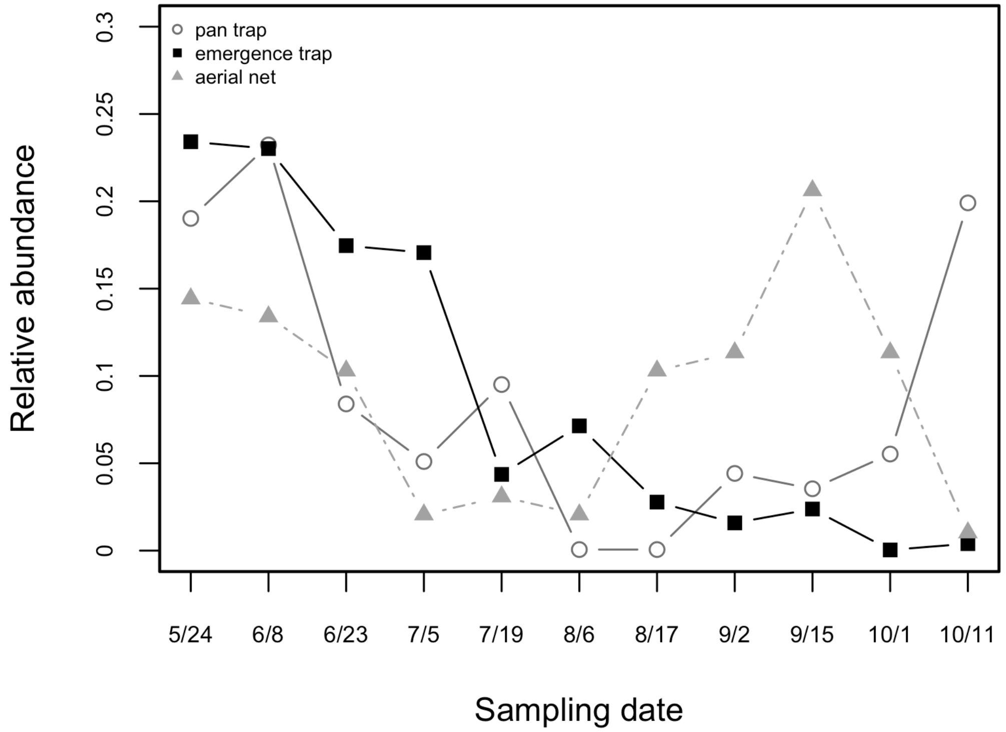


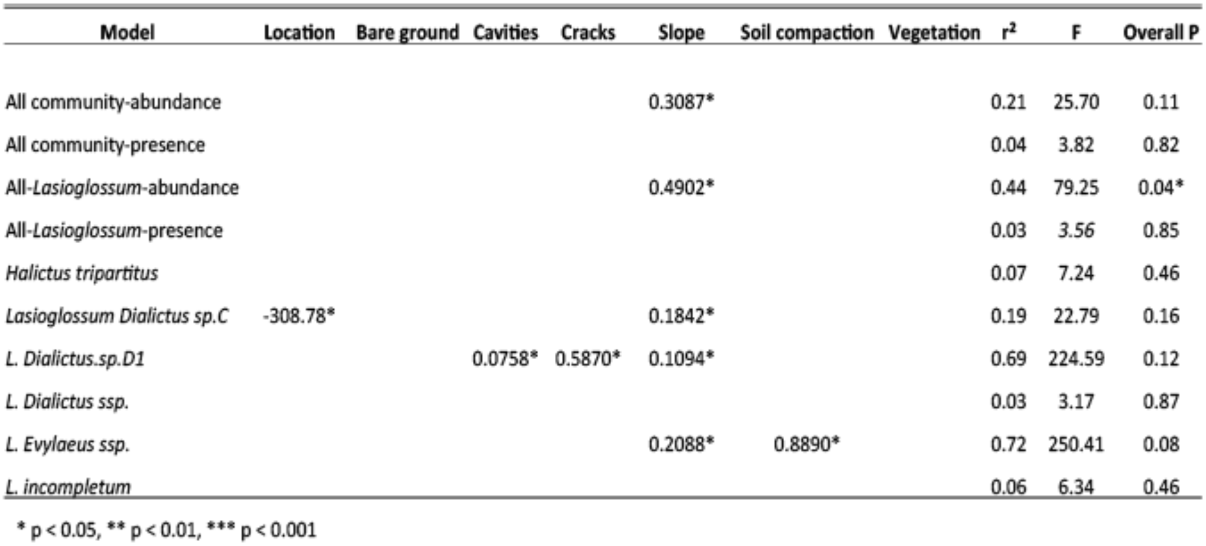
Fig. 4. Relative abundance of specimens collected over the study period using pan traps, netting, and emergence traps.

Tables

Table 1. Nesting variables used for quantifying nesting resources within emergence traps (adapted from Potts et al., 2005).

Nesting Variable	**Metric**
Bare ground	% bare exposed soil
Cavities	Any kind of hole in the ground, divided into two categories: number of small (< 2 cm) and large (> 2 cm)
Cracks	% of plot with cracks, for example, if a crack spanned the length of the trap but was < 1 cm it would be marked as 1%
Litter	% dead vegetation or leaf litter
Slope	Divided into three catagories: percent slope in plot < 30°, 30 - 60°, > 60° Slopes > 60° were typically protrusions in soil
Soil Compaction	A measure of surface soil resistance (0 - 4.5 kgf cm-2) taken with a soil penetrometer (Model No. 77114,. Forestry Suppliers, Inc., Jackson, Mississippi, USA)
Vegetation	% living vegetative cover

Table 2. We constructed distance matrices using a multiple regression on Bray-Curtis distance matrices to evaluate the spatial distribution of resources on nesting incidence and abundance for species with occurrences > 5. The values are Bray-Curtis dissimilarities. A complete table may be found in the Appendix (Table 4).



Model	Location	Bare ground	Cavities	Cracks	Slope	Soil compaction	Vegetation	r^2	F	Overall P
All community-abundance					0.3087*			0.21	25.70	0.11
All community-presence								0.04	3.82	0.82
All-*Lasioglossum*-abundance					0.4902*			0.44	79.25	0.04*
All-*Lasioglossum*-presence								0.03	*3.56*	0.85
Halictus tripartitus								0.07	7.24	0.46
Lasioglossum Dialictus sp.C	-308.78*				0.1842*			0.19	22.79	0.16
L. Dialictus.sp.D1			0.0758*	0.5870*	0.1094*			0.69	224.59	0.12
L. Dialictus ssp.								0.03	3.17	0.87
L. Evylaeus ssp.					0.2088*	0.8890*		0.72	250.41	0.08
L. incompletum								0.06	6.34	0.46

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Appendix A: Supplement

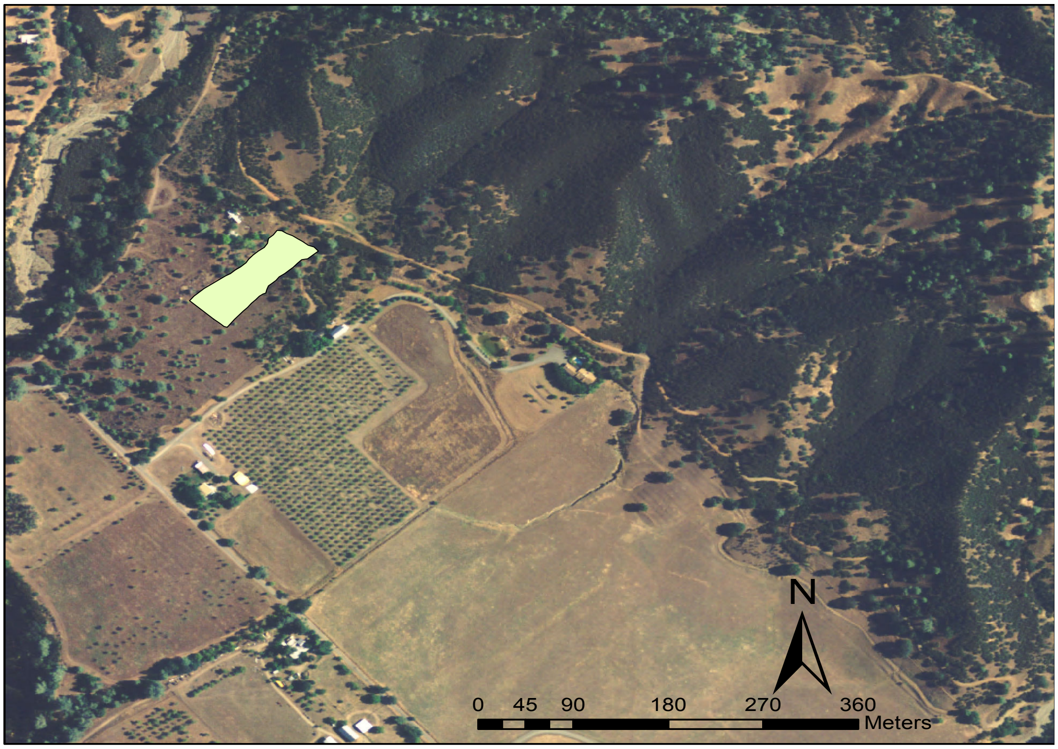


Fig. 1. The 4800m^2 study area bordered foothill chaparral habitat and a seasonal creek to the northwest. It was embedded in a matrix that also contained agricultural and grazing lands, as well as sparse housing.

Fig. 2. Emergence traps (BugDorm) in study landscape.

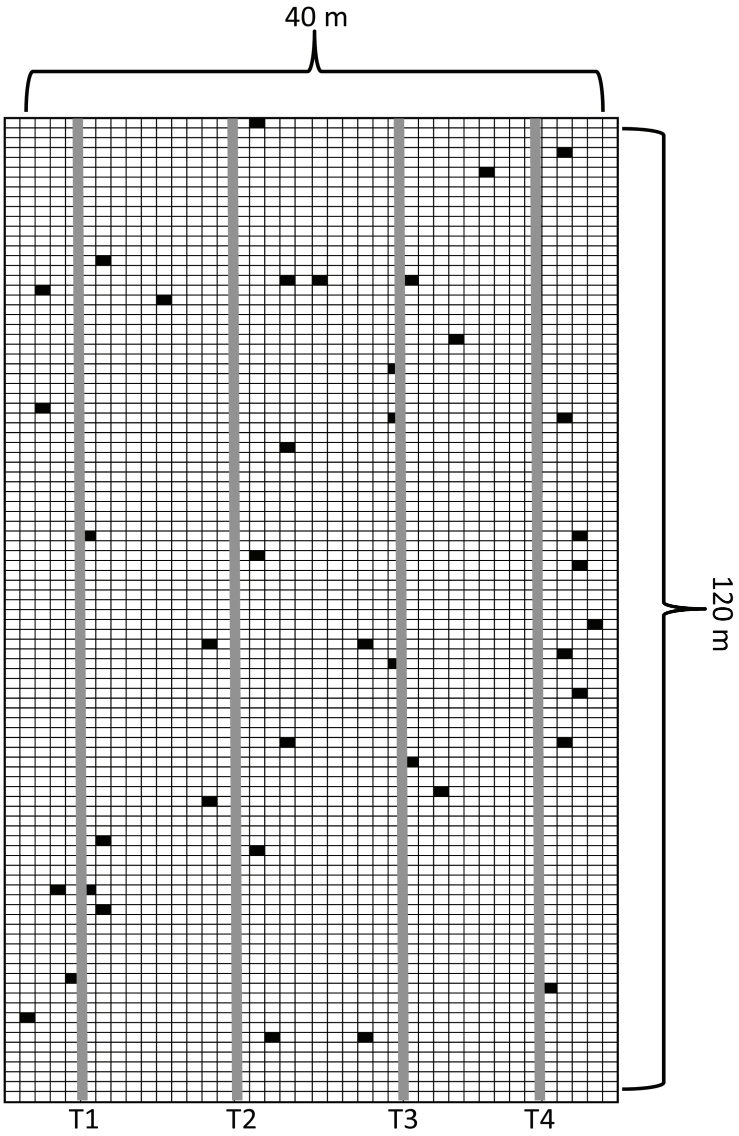


Fig. 3. We gridded our study area with 1 m^2 grid cells and placed 40 emergence traps in randomly selected cells. Black boxes represented trap locations. We pan trapped bees with 6 pan traps (alternating blue, white, yellow) along 4 parallel transects (T1 – T4) for a total of 24 pan traps within the site. Bees were netted in floral patches throughout the entire study area using variable transect walks.

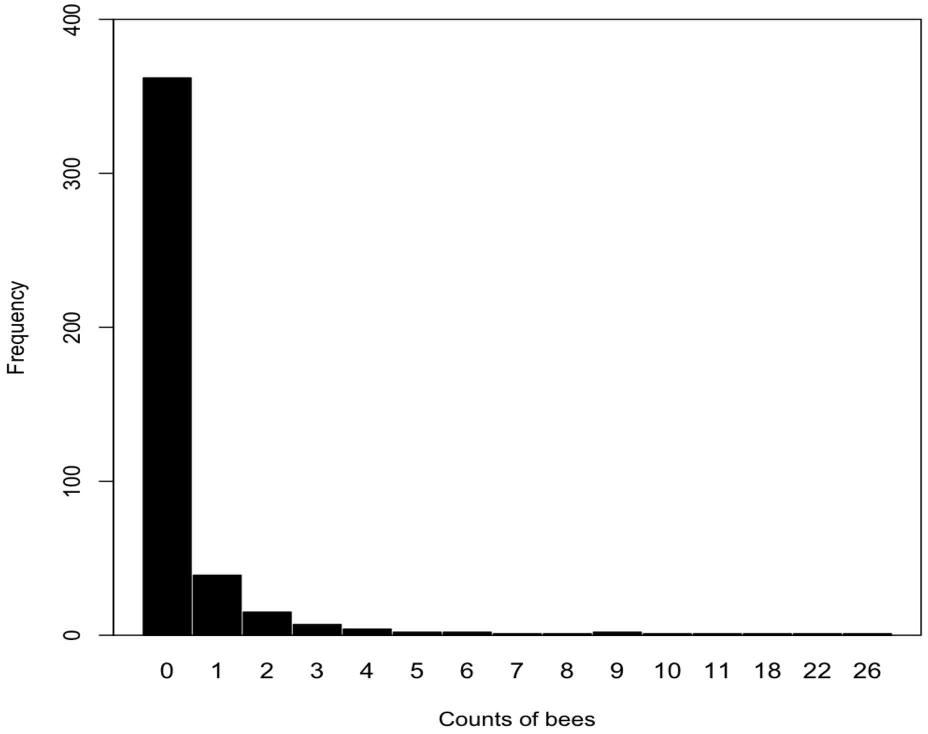


Fig. 4. Over the entire study period, the emergence trap sampling method yielded a high number of zeros, indicative of traps without any bees collected. Such skewed, long-tailed data is typical of count data, and is best analyzed with models that increase the probability mass of zeros.

Table 1. Correlation matrix of nesting resources. Nesting proxies were highly intercorrelated, for example, percent litter (2) was significantly positively and negatively correlated to six other resources, making interpretation challenging. We dropped this term, and other highly correlated terms from our final model. Values are Pearson correlations.

Nesting Characteristic	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
% Vegetative Cover (1)	1								
% Litter (2)	-0.4416**	1							
% Bare ground (3)	0.1402	-0.9470***	1						
% Cracked (4)	-0.0940	-0.1776	0.2248	1					
# Cavities < 2 cm (5)	-0.0531	-0.5072**	0.5691***	0.2548	1				
# Cavities > 2 cm (6)	-0.0375	-0.3385**	0.3824*	0.0356	0.0250	1			
% Slope < 30° (7)	-0.0056	0.3860*	-0.4196**	-0.2810	-0.6241***	-0.0150	1		
% Slope 30-60° (8)	-0.0067	-0.3613*	0.3965*	0.2106	0.5509***	-0.0173	-0.9688***	1	
Soil hardness (9)	0.1485	0.0031	-0.0520	-0.2707	-0.1993	0.0611	0.2417	-0.2075	1

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 2. The number of specimens from each species collected with the different sampling methods over the entire study period. Many species of *Lassioglossum* are not identifiable to species, thus were sorted to morphospecies. Data concerning nest location was originally compiled by Neal Williams.

	5/24			6/8			6/23			7/5			7/19			8/6			8/17			9/2			9/15			10/1			10/11		
Species	**etrap**	**net**	**pan**	**etrap**	**net**	**pan**	**etrap**	**net**	**pan**	**etrap**	**net**	**pan**	**etrap**	**net**	**pan**	**etrap**	**net**	**pan**	**etrap**	**net**	**pan**	**etrap**	**net**	**pan**	**etrap**	**net**	**pan**	**etrap**	**net**	**pan**	**etrap**	**net**	**pan**
Above-ground nesters																																	
Anthidium utahense								1						1																			
Apis mellifera			10			3																											1
Ashmeadiella aridula astragali														2																			1
Ashmeadiella timberlakei						1																											
Ceratina arizonensis						1														1				1									
Ceratina nanula									1																								
Chelostoma marginatum						1																											
Hoplitis hypocrita					1																												
Hoplitis producta gracilis						1		1																									
Megachile angelarum								1																									
Megachile apicalis								1						2						3			1										
Megachile frugalis									1								1							1			1						
Megachile gentilis					1																												
Osmia albolateralis		1				1																											
Osmia brevis						1																											
Osmia granulosa									1																								
Osmia nemoris			3			3			1																								
Parasites																																	
Sphecodes sp. 1										2																							
Sphecodes sp. C	4																																
Sphecodes ssp.	2				1																												
Xeromelecta californica					1																												
Below-ground nesters																																	
Agapostemon texanus															1																		
Andrena caerulea	1																																
Andrena candida	1																																
Andrena cerasifolii				3																													
Andrena medionitens	3			1																													
Andrena w-scripta		1																															
Anthophora urbana																				4			2			8			7			1	
Bombus californicus		1																															
Bombus vosnesenskii		1																															
Calliopsis cincta hurdi			1																														
Calliopsis fracta		1				2			1																								
Diadasia enavata																											1						
Eucera actuosa			7			6									1																		
Halictus farinosus						1																											
Halictus ligatus			1			1																											
Halictus tripartitus	1	1	29		1	52	5		17			18			28	2		2		1	3		4	14		8	9		2	7			22
Hylaeus calvus		3																															
Hylaeus mesillae								1																									
Lasioglossum (Dialictus) sp. B																														1			
Lasioglossum (Dialictus) sp. C	23	1	4	21		5	9			14																							
Lasioglossum (Dialictus) sp. D1				3			6																										
Lasioglossum (Dialictus) sp. F			2		1																												1
Lasioglossum (Dialictus) ssp.	20	4		15	4	2	23		1	7													1	2			1			1			
Lasioglossum (Evylaeus) sp. F			2																														
Lasioglossum (Evylaeus) sp. G																																	1
Lasioglossum (Evylaeus) sp. H						1																											
Lasioglossum (Evylaeus) ssp.	2			15	1																												
Lasioglossum incompletum	2		17			21	1		13			3	11		12	16		1	7			4	1		6		4	1		13	1		51
Lasioglossum mellipes										3																							
Lasioglossum tegulariforme			1												1																		2
Melissodes lupina									2																					3			7
Melissodes stearnsi												1					1			1			2	2		3			2				
Perdita trisignata ornata			8		9								17																				

Table 3. Number of specimens netted off plant species during each sampling round.

Plant Species	5/24/11	6/8/11	6/23/11	7/5/11	7/19/11	8/6/11	8/17/11	9/2/11	9/15/11	9/21/11	10/11/11	TOTAL
Centaurea solstitialis					3	2	2					7
Clarkia purpurea												0
Croton californicus								3				3
Daucus pusillus												0
Erodium cicutarium												0
Eriogonum californica	11	1										12
Heteromeles arbutifolia			6									6
Hypochaeris radicata												0
Lotus scoparius	3	12	4	2								21
Trichostema lanceolatum												0
Trifolium fragiferum							8	8	20	11	1	48

Table 4. Bray-Curtis Dissimilarity scores for all nesting resources used in the MRM assessing spatial distribution of resources.

Model	Location	Bare ground	Cavities	Cracks	Slope	Soil hardness	Vegetation	r^2	F	Overall P
All community-abundance	781.1718	-0.0273	-0.2849	-0.9008	**0.3087***	-1.2865	-0.1015	0.21	25.70	0.11
All community-presence	-8.9759	-0.0013	-0.0062	-0.0456	-0.0028	-0.0525	-0.0062	0.04	3.82	0.82
All-*Lasioglossum*-abundance	-719.8644	-0.015913	0.0082	0.6390	**0.4902***	0.8976	0.014739	0.44	79.25	**0.04***
All-*Lasioglossum*-presence	-11.9356	-5.5467e-4	-0.0068	-0.0044	-0.0026	-0.0597	-0.0011	0.03	*3.56*	0.85
Halictus tripartitus	-13.0955	0.0037	-0.0056	0.1924	0.0016	-0.0435	-0.0049	0.07	7.24	0.46
Lasioglossum Dialictus sp.C	**-308.78***	-0.0151	-0.1390	-0.6353	**0.1842***	-0.3514	-0.007	0.19	22.79	0.16
L. Dialictus.sp.D1	-0.0110	0.0045	**0.0758***	**0.5870***	**0.1094***	5.7929	0.0117	0.69	224.59	0.12
L. Dialictus ssp.	-152.96	-0.0055	-0.0535	-0.3573	0.0359	-0.0494	0.0323	0.03	3.17	0.87
L. Evylaeus ssp.	-222.5933	0.0057	0.0996	0.9024	**0.2088***	**0.8890***	0.01456	0.72	250.41	0.08
L. incompletum	-61.3667	-0.0058	0.0836	-0.1742	0.0113	-0.2062	-0.0318	0.06	6.34	0.46

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$
Note: Significant values are bolded

Emergence traps proved to be a highly successful method for randomly sampling ground-nesting wild bees and correlating specific nesting resources to nest incidence. In the next chapter, I utilize emergence traps to ask whether hedgerow plantings increase both nesting resources and nesting rates of ground-nesting wild bees. If hedgerow plantings are able to do this, then simply increasing vegetative diversity is likely a sufficient for maintaining wild pollinator populations. If, however, hedgerow plantings do not alter nesting resources and/or rates, it indicates that further measures need to be taken in order to ensure wild pollinators are able to reproduce and persist in intensive agricultural landscapes.

Chapter 3

Hedgerow presence does not enhance indicators of nest-site habitat quality or nesting rates of ground-nesting bees

Hillary S. Sardiñas, Lauren Poinsio, and Claire Kremen

Accepted for publication
Restoration Ecology
November 2015

Abstract:
A major challenge in habitat restoration is targeting the key aspects of a species' niche for enhancement, particularly for species that use a diverse set of habitat features. However, restoration that focuses on limited aspects of a species' niche may neglect other resources that are critical to population persistence. We evaluated the ability of native plant hedgerows, planted to provide pollen and nectar resources for wild bees in agricultural landscapes, to provide suitable nesting habitat and enhance nesting rates of ground-nesting bees. We found that, when compared to unmanaged field edges (controls), hedgerows did not augment most indicators of nest habitat quality (bare ground, soil surface irregularity, soil hardness), although coarser soils were associated with higher incidence and richness of nesting bees. Hedgerows did not augment nesting rates when compared to control edges. Although all the bee species we detected nesting were also found foraging on floral resources, the foraging versus nesting assemblages found within a site were highly dissimilar. These results may reflect sampling error; or, species found foraging but not nesting in hedgerows could be utilizing hedgerows as "partial habitats," nesting outside hedgerow plantings but foraging on the floral resources they provide. We conclude that while hedgerows are known to provide critical floral resources to wild bees especially in resource-poor intensive agricultural landscapes, simply increasing vegetative diversity and structure may not be simultaneously enhancing nesting habitat for ground-nesting bees.

Keywords: Agriculture; Apoidea; Conservation; Emergence traps; Field edges; Nesting resources; Pollination services; Restoration.

Introduction

For restoration projects aimed at promoting specific species or guilds, it is important to enhance habitat characteristics on which target taxa rely (Miller & Hobbs 2007). Yet the autecology of many species, particularly invertebrates, is complex and often poorly understood (Murray et al. 2009). Thus, a restoration project may elect to focus on readily managed factors known to affect a species' life-history. However, if only one dimension of a species' niche is restored, other factors critical to their establishment may be inadvertently neglected. For species reliant on restored fragments, an absence or lack of specific features could cause an area either to be unoccupied or to function as a sink (Pulliam 1988). Determining whether restoration of some habitat elements can enhance other key habitat features may be important for sustaining local populations of the species of interest.

Wild bees (Hymenoptera: Apoidea) are critically important species in natural and agricultural areas (Memmott et al. 2004; Garibaldi et al. 2013), and as such, have been the focus of habitat enhancement projects (Dixon 2009; Menz et al. 2011; Winfree 2010; Garibaldi et al. 2014). Pollen and nectar are the sole food supply for bee larvae, therefore floral blooms are essential for bee reproduction. In addition, bees require nesting substrates (e.g., appropriate soil conditions for below-ground nesters; pithy stems or cavities in wood for above-ground nesters) and nesting materials (e.g., mud or leaves to construct partitions between brood cells). Bees are central place foragers; thus floral and nesting resources must be within flight range of their nest location (Westrich 1996). Identifying appropriate floral resources is easier than targeting nesting habitat, since nest sites are hard to locate and the nesting needs of many bee species remains unknown (Roulston & Goodell 2011). The majority of pollinator-related restoration projects therefore focus on floral diversity and abundance (Winfree 2010; Garibaldi et al. 2014), and not nesting resources.

Hedgerows are a common habitat enhancement technique targeted at augmenting wild pollinator populations in agricultural landscapes. Hedgerows are linear plantings of shrubs and forbs that can be added to field margins (Long & Anderson 2010); they may contain native or non-native species, or a mixture of both. Hedgerows are multifunctional, acting as windbreaks, filter strips and erosion control buffers (Wratten et al. 2012). Beneficial insects (e.g., wild pollinators or natural enemies of crop pests) prefer native plants are (Isaacs et al. 2009; Morandin & Kremen 2013a), therefore, when hedgerows are planted with the goal of augmenting habitat for beneficial insects they generally contain numerous flowering native plant species (Long et al. 1998; Long & Anderson 2010). By planting species with overlapping bloom periods lasting from early spring to later summer, hedgerows provide stable, attractive floral resources throughout the growing season (Hannon, Sisk 2009; Gareau et al. 2013; Morandin & Kremen 2013b; Morandin et al. 2014).

Since hedgerow enhancement specifically involves increasing local floral availability and diversity, it is unclear whether hedgerow presence also improves wild bee nesting habitat. Hedgerows introduce woody plants into agricultural landscapes often lacking vegetative and structural diversity. Morandin & Kremen (2013b) found that hedgerows increased the amount of dead wood over unenhanced field edges. A subsequent study found that hedgerow maturation led to higher occurrences of above-ground nesting bees in field edges containing hedgerows (Kremen & M'Gonigle 2015). The presence of perennial shrubs in hedgerows can limit soil disturbances in field edges, such as disking, that may negatively impact wild bee nesting (Brodt et al. 2009). Hedgerows may also suppress weed populations (Wilkerson 2014), potentially increasing the proportion of available bare ground. These changes might be expected to promote ground-nesting bees; in particular, bare ground is a site characteristic that has been linked to enhancing the abundance of below-ground nesting bees (Potts et al. 2005; Sardiñas & Kremen 2014). However, evaluation of habitat enhancement projects to-date has focused on floral resources. There therefore exists a pressing need for assessments of nesting resources in pollinator-focused restoration projects (Winfree 2010).

In this study we examine the ability of hedgerows to increase nesting habitat for ground-nesting wild bees. We characterize nesting habitat by quantifying characteristics thought to be linked to nesting incidence (hereafter "nesting indicators;" Potts et al. 2005; Grundel et al. 2010; Sardiñas & Kremen 2014). First, we determine whether hedgerows enhance nesting indicators when compared to unenhanced field edges. Next, we ask whether differences in nesting indicators influence the nesting rates of wild ground-nesting bees. Finally, we compare the overlap in the composition of communities found nesting with those visiting floral resources at these sites to determine whether bee species are utilizing floral resources within hedgerows but not nesting there.

Methods

Study system

We conducted our study in Yolo County, located in California's Northern Central Valley. The region is characterized by intensive agricultural production of orchard and row crops and contains little remnant natural habitat (Sardiñas & Kremen 2015; Kremen & M'Gonigle 2015), although it also contains a relatively high density of hedgerow enhancements (Brodt et al. 2009). There is little topographic variation in the farmed areas, with most slopes < 2% (NRCS USDA 2014). Soils are typically well-drained silty loam or silty clay loam (NRCS USDA 2014).

Hedgerows in our study were at least five years post-planting and contained a mixture of perennial shrubs, perennial forbs and annual forbs (see Supplement for plant list, Table S1; Long & Anderson 2010). The majority of plant species are California natives, though hedgerows also contained numerous colonizing weedy species (Table S1). Although there was some variation in hedgerow management (e.g. hand weeding versus spot herbicide treatment), many factors, such as use of pre-emergent herbicide and irrigation, were similar (Wilkerson 2014). Unrestored controls are also managed in a variety of ways, including mowing, disking, burning, herbicide treatment or no active management (Brodt et al. 2009; Morandin & Kremen 2013b; Garbach & Long, *unpublished data*).

We sampled eight hedgerows and eight unenhanced field edges (hereafter referred to as controls; Figure 1S). We sampled each site three times, twice in year 1 and once in year 2, between May and August, to capture variation in the bee community over the spring and summer flight seasons, as well as to document any changes to nesting resource availability. Sites were a minimum of 1 km apart to ensure the majority of the bee individuals visiting a site were unlikely to forage between sites (Greenleaf et al. 2007).

Sampling the Bee Community

We focused on below-ground nesting bees because the majority of bees nest beneath the soil and locating the nests of above-ground nesting bees is exceedingly challenging (Roulston & Goodell 2011; Sardiñas & Kremen 2014). We sampled the below-ground nesting community using 0.6 m^2 emergence traps (e-traps; Bug Dorm; Sardiñas & Kremen 2014). E-traps were fitted with jars at their apex filled with soapy water to kill emerging insects. We set e-traps at dusk to ensure that bees had returned to their nest sites; the e-traps were removed the following afternoon, approximately 20 hours after being set. We only set e-traps if weather conditions the following day were predicted to have clear skies, temperatures over 18°C and wind speeds < 2.5 m/s to ensure that weather conditions would not impede insect activity. We placed thirty e-traps in each site during each sampling round. Ten e-traps were placed 30 m apart along three transects, one to either side of the hedgerow and one in line with hedgerow plantings (Figure 1). If a shrub conflicted with placement of an e-trap, the e-trap was set alongside the plant as close to the base of the shrub as possible. The sides of each e-trap were weighted down to prevent bees from entering or escaping.

To document the bee species foraging on floral resources within our study sites, we netted bees from inflorescences for one hour, excluding time spent handling specimens. All sampling was conducted between 08:00 and 14:00 hours. Net surveys were performed within 10 days of e-trap sampling under allowed weather conditions.

Sampling of Nesting Habitat

We visually estimated indicators of nest-site quality within e-traps following Sardiñas & Kremen (2015) and Potts et al. (2005). We focused on indicators that have been found to significantly impact nesting rates: percent bare ground, variation of slope of the ground, surface soil compaction, and soil particle size (Table 1; Sardiñas & Kremen 2014; Grundel et al. 2010; Potts et al. 2005). Farmed areas in the California Central Valley are generally flat, thus the sloping ground within the e-traps was indicative of soil surface irregularity, not topographic variation. Soil surface irregularity has been found to heighten nesting rates for some species (Wuellner 1999). To capture soil surface heterogeneity, we used the coefficient of variation in slope (CV). To evaluate soil particle size, we collected two samples at 10 cm depth at each site. Samples were homogenized, dried in a forced air oven at 40°C for two days, and sieved to remove coarse (> 2mm) particles and other debris. We then calculated average particle size (microns) with a laser diffraction particle size analyzer (Sequoia LISST Portable XLR).

Statistical Analysis

We evaluated sample coverage from e-traps using species accumulation curves in the R package vegan (Oksanen et al. 2013; R version 3.1.2). To determine whether differences in the characteristics of nesting habitat translated to differences in the community composition of ground-nesting species, we calculated the pair-wise dissimilarity between sites for both species composition and nesting indicators (Anderson et al. 2011; Gower 1971; Laliberte et al. 2010). We then assessed the correlation between the dissimilarity of species and nesting indicators using a Mantel test.

We determined whether hedgerows increased nesting habitat using generalized linear mixed models (Bates et al. 2014). In each model, the nesting indicator was the dependent variable, site status (hedgerow or control) was the independent variable, and Site was a random factor.

To assess the influence of nesting indicators on below-ground nesting we constructed a zero-inflated mixed model with a binomial error (Fournier et al. 2012). We assessed nesting incidence rather than abundance because we collected many social bee species that share nests (Table S2), we were therefore unable to determine the number of independent nests. To test whether hedgerows affected nesting rates, we included site type (hedgerow or control) as an explanatory variable. In addition, we included Julian date and Julian date square to account for the seasonal phenology of bees (Kremen & M'Gonigle 2015). All continuous variables were scaled.

Next, we examined species richness (rarified; Chao et al. 2005) within e-traps using a generalized linear mixed model with a Poisson error distribution and the same explanatory variables as the incidence models (Bates et al. 2014). Rarified richness was rounded so that a generalized linear mixed model with Poisson error could be fit.

We then evaluated whether nesting indicators influenced the incidence and rarified richness of foraging bees collected using aerial netting from plants in bloom in hedgerow and control sites using the same model structure, but including a random effect of species. We then compared the assemblage of bees collected in e-traps (hereafter "nesting bees") to the assemblage of bees collected with netting (hereafter "foraging bees") in a PerMANOVA using a dissimilarity estimator that incorporates species abundances while also accounting for unobserved species (Chao et al. 2005; Oksanen et al. 2013). This was visualized using non-metric dimensional scaling (NMDS).

For all models we used model validation procedures to ensure that the models were not overdispersed and did not have inflated type I error rates (Ives 2015; Sardiñas et al., *in press*). We included only female bees of ground-nesting species in all analyses (both nesting and foraging) because male bees are not indicative of nesting rates and may only be resting in vegetation (Kim et al. 2006). We did not examine the availability of nesting resources for above-ground nesting species because we did not collect above-ground nesting species in e-traps. We also excluded any parasitic bees, as their distributions are linked to that of their host species and including them could double-count the resources preferred by their host species.

Results

Nesting bees

We collected 893 ground-nesting bees from 10 species in e-traps (Table S2). Ninety-nine percent of all bees collected in e-traps were in the genera *Halictus* and *Lasioglossum*. Rarefaction showed that species accumulation leveled off by 30 traps— the number we set in each site during each sampling round— in half of the sites we sampled (Figure S2). This suggests that increased sampling with e-traps likely would have detected additional species. An average of 39% of e-traps (SE = 6.4) contained below-ground nesting bees per site/sampling round combination.

Nesting habitat indicators were highly similar in control and hedgerow sites (Table 2; Figure S3), suggesting that hedgerow plantings did not alter these soil- or nesting-related characteristics. In fact, ground-nesting rates were significantly lower in sites containing hedgerow enhancements than in unenhanced control edges (Table 3). There was a downward trend in both nesting incidence and the richness of ground-nesting species in hedgerows (Table 3; Figure 2). Seasonality (Julian date) had the strongest effect on nesting, with nesting bees peaking in incidence in late June. Soils with finer particles (clay- and silt-based soils) had marginally negative effects on nesting (Table 3). Nesting indicators did not strongly impact nesting; ground-nesting bee community dissimilarity was not correlated with site to site dissimilarity in nesting characteristics (r = -0.13, P = 0.76), indicating a lack of correlation between nesting species and the indicators we measured.

Foraging bees

We netted 425 ground-nesting bees from 20 species foraging on floral resources in hedgerow and control sites (Table S2). The Chao1 estimated species richness of foraging ground-nesting bees was 38.66 ±14.84. Although the assemblage of ground-nesting species was a subset of the overall foraging community, the composition of nesting versus foraging species assemblages of ground-nesters collected at the same site were highly differentiated (Figure 3). Further, the assemblages of ground-nesting bees in control and hedgerow edges more closely resembled one another than they did the foraging assemblage in the same site types. Soil hardness, soil particle size, and Julian date all had marginal effects on the richness of foraging ground-nesting bees, while foraging incidence responded to surface soil compaction (Table 3).

Discussion

Hedgerow presence did not dramatically alter the underlying site conditions for the nesting indicators we measured. Nesting indicators either did not vary among sites (e.g., soil hardness and slope variability), or variation within site type (hedgerow versus control) was higher than between site type (e.g., bare ground). Weed density likely contributed to the high degree of similarity in percent bare ground in hedgerows and controls, despite the presence of woody shrubs in hedgerow that have the potential to shade out weedy species (Wilkerson 2014).

One potential reason for the high degree of similarity between nesting indicators could be due to the location sampled by e-traps in hedgerow and control edges. By sampling adjacent to, but not directly underneath hedgerow plants, we may have inadvertently measured nesting indicators in locations where there was little difference between hedgerow and control sites. The lack of turnover of nesting species that we observed across sites could be a result of the low variation in nesting characteristics between sites, which could be attributable to sampling design, though because of the very low variability likely represents nesting indicator availability. This observed homogeneity of nesting habitat within agricultural field margins may function as an ecological filter, limiting colonization by species with different nesting requirements (Ponisio et al., *in press*).

Hedgerows may, however, function as a refuge for bees nesting in agricultural areas. Hedgerows contain undisturbed ground that is free from tilling and herbicide use, methods frequently used to control weeds in unenhanced field margins (Wilkerson 2014). Although ground-nesting bees nest in hedgerow and non-hedgerow sites in equal numbers, their young may be more successful in hedgerow sites. Tilling in nest sites within agricultural fields leads to high mortality rates in ground-nesting bee offspring (Ullmann 2015). To date, nesting success of ground-nesting bees in hedgerows has not been evaluated.

Ground-nesting wild bees did not respond to most of the nesting indicators that we measured, except for soil particle size. Soils with smaller particles adversely impacted nesting rates. In our study system soils are predominantly silty clay loams (NRCS USDA 2014). Clay-based soils have been found to be the least-utilized soils for nesting bee species (Cane 1991), and may limit the species that can colonize agricultural field margins in our area. The most abundant bees in our e-trap samples (sweat bees in the genera *Halictus* and *Lasioglossum*) may be less sensitive to poor soil conditions, contributing to their dominance in our study region (Morandin & Kremen 2013b).

The nesting biology of the majority of bee species remains undescribed (Roulston & Goodell 2011), therefore the range of variables influencing wild bee nesting behavior is largely unknown. Although we focused on nesting characteristics that have been previously shown to influence community composition (Potts et al. 2005; Grundel et al. 2010, Sardiñas & Kremen 2014), most were not important factors affecting nesting in the agricultural field edges we studied, or differentiating among hedgerows and controls. Other factors that we did not measure may influence nesting, such as insolation (Potts & Wilmer 1997) or soil moisture (Xie et al. 2013).

The edaphic characteristics preferred by wild bees for nesting may be slow to respond to restoration efforts that do not directly target soil properties. For example, although hedgerows in our study were between 5– 12 years post-planting (Morandin & Kremen 2013b; Sardiñas & Kremen 2015), this short time frame might not be sufficient to affect significant changes in soils in agricultural field edges. Thus, once edaphic conditions suitable for bee nesting are identified (such as with alkali bees; Stephen 1960), specific techniques aimed at creating such conditions may need to be implemented at restoration sites.

We collected many species of bees foraging in hedgerows that we did not capture in e-traps. Foraging bees that we did not encounter in our e-trap sample could have been nesting elsewhere in the landscape but utilizing floral resources provided by hedgerows. Nearby natural or semi-natural habitat, such as rangelands, have been suggested as potential nesting habitat (Kremen et al. 2002). In addition, some bee species have been shown to nest directly within agricultural fields (Kim et al. 2006; Sardiñas et al., *in press*). In floral-limited landscapes, including intensively managed agriculture, bees may forage long distances between their nest sites in other landscape features and hedgerow plantings (Zurbuchen et al. 2010). Alternately, foraging species could have been nesting in our study sites but were undetected. This lack of detection could be driving the similarity in nesting incidence and richness between hedgerow and control sites.

Our sample size for nesting bees was small and represented only a few of the species found foraging within hedgerows. During each sampling round, emergence traps covered less than 1% of each hedgerow site. Despite the leveling off of most sampling effort curves, heightened sampling would have likely increased capture rates, which may have not only led to more overlap between species collected through netting, but also altered the trends we observed related to response to nesting indicators.

Since bees are mobile, small-scale habitat enhancement projects in heterogeneous landscapes or natural habitats may not need to focus on enhancing nesting habitat, as bees may be able to forage from their nesting sites in adjacent habitat into the restored site to utilize available floral resources (Westrich 1996). In highly altered, homogenous landscapes, such as intensified agricultural areas, nesting habitat may be limited, therefore improving local nest-related conditions may be critical. Our findings suggest that only a subset of bees nest within hedgerow plantings, while many more species forage there. These foraging species may use hedgerows as a "partial habitat" (Westrich 1996). Although hedgerows may only provide some of the resources required for the majority of the species utilizing hedgerows, diverse hedgerows providing sequential floral resources likely contribute to maintaining local bee populations (M'Gonigle et al., *in press*) and communities (Kremen & M'Gonigle 2015). In order to maintain and enhance pollinator populations it is important to continue increasing floral diversity in agricultural regions while also exploring alternate methods for enhancing nesting habitat.

Literature Cited

Anderson MJ, Crist TO, Chase JM, Velland M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV, Comita LS, Davies KF, Harrison SP, Kraft NJ, Stegen JC, Swenson NG (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology Letters 14:19-28

Bates D, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using Eigen and S4. ArXiv e-print; Journal of Statistical Software. http://arxiv.org/abs/1406.5823

Brodt S, Klonsky K, Jackson L, Brush SB, Smukler S (2009.) Factors affecting adoption of hedgerows and other biodiversity-enhancing features on farms in California, USA. Agroforestry systems 76:195-206

Cane JH (1991) Soils of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth and climate. Journal of the Kansas Entomological Society: 406-413

Cane JH (2011) Meeting wild bees' needs on Western US rangelands. Rangelands 33:27-32

Chao, A, Chazdon RL, Colwell R (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters 8:148-159

Dixon KW (2009) Pollination and restoration. Science 325:571

Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder M, Nielsen A, Sibert J (2012) AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim. Methods Softw. 27:233-249

Gareau TLP, Letourneau DK, Shennan C (2013) Relative densities of natural enemy and pest insects within California hedgerows. Environmental Entomology 42:688-702

Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, Cunningham SA, Kremen C, Carvalheiro LG, Harder LD, Afik O, Bartomeus I, Benjamin F, Boreux V, Cariveau D, Chacoff NP, Dudenhöffer JH, Freitas BM, Ghazoul J, Greenleaf S, Hipólito J, Holzschuh A, Howlett B, Isaacs R, Jovorek SK, Kennedy CM, Krewenka KM, Krishnan S, Mandelik Y, Mayfield MM, Motzke I, Munyuli T, Nault BA, Otieno M, Peterson J, Pisanty G, Potts SG, Rader R, Ricketts TH, Rundlöf M, Seymour CL, Schüepp C, Szentgyörgyi H, Taki H, Tscharntke T, Vergara CH, Viana BF, Wanger TC, Westphal C, Williams NM, Klein A-M (2013) Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. Science 339:1608–1611

Garibaldi LA, Carvalheiro LG, Leonhardt SD, Aizen MA, Blaauw BR, Isaacs R, Kuhlmann M, Kleijn D, Klein A-M, Kremen C, Morandin L, Scheper J, Winfree R (2014) From research to action: enhancing crop yield through wild pollinators. Frontiers in Ecology and the Environment 12:439–447

Gower JC (1971) A general coefficient of similarity and some of its properties. Biometrics:857-871

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153:589–596

Grundel R, Jean RP, Frohnapple KJ, Glowacki GA, Scott PE, Pavlovic NB (2010) Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. Ecological Applications 20:1678-1692

Hannon LE, Sisk TD (2009) Hedgerows in an agri-natural landscape: potential habitat value for native bees. Biological Conservation 142:2140-2154

Isaacs R, Tuell J, Fiedler A, Gardiner M, Landis D (2009) Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. Frontiers in Ecology and the Environment 7:196-203.

Ives AR (2015) For testing the significance of regression coefficients, go ahead and log-transform count data. Methods in Ecology and Evolution 7:828-835

Kim J, Williams NM, Kremen C (2006) Effects of cultivation and proximity to natural habitat on ground-nesting native bees in California sunflower fields. Journal of the Kansas Entomological Society 79:309-320

Li YY, Shao MA (2006) Change of soil physical properties under long-term natural vegetation restoration in the Loess Plateau of China. Journal of Arid Environments 64:77-96

Kremen C, M'Gonigle LK (2015) Small-scale restoration in intensive agricultural landscapes supports more specialized and less mobile pollinator species. Journal of Applied Ecology (in press)

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299-305

Long R, Corbett A, Lamb C, Reberg-Horton C, Chandler J, Stimmann M (1998) Beneficial insects move from flowering plants to nearby crops. California Agriculture 52:23-26

Long R, Anderson J (2010) Establishing hedgerows on farms in California. UCANR Publications, Berkeley, CA, USA.

M’Gonigle LK, Ponisio LC, Cutler K, Kremen C (2015) Habitat restoration promotes pollinator persistence and colonization in intensively-managed agriculture. Ecological Applications (in press)

Memmott J, Waser NM, Price MV (2004) Tolerance of pollination networks to species extinctions. Proc. R. Soc. Lond. B. 271:2605-2611

Menz MH, Phillips RD, Winfree, R, Kremen C, Aizen MA, Johnson SD, Dixon KW (2011) Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. Trends in Plant Science 16:4-12

Miller JR, Hobbs RJ (2007) Habitat restoration—do we know what we’re doing? Restoration Ecology 15:382-390

Morandin LA, Kremen C (2013a) Bee preference for native versus exotic plants in restored agricultural hedgerows. Restoration Ecology 21:26-32

Morandin LA, Kremen C (2013b) Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. Ecological Applications 23:829-839

Morandin LA, Long RF, Kremen C (2014) Hedgerows enhance beneficial insects on adjacent tomato fields in an intensive agricultural landscape. Agriculture, Ecosystems & Environment 189:164-170

Murray TE, Kuhlmann M, Potts SG (2009) Conservation ecology of bees: populations, species and communities. Apidologie 40:211-236

NRCS USDA (2014) Yolo County, California Survey Area Version 10. Web Soil Survey. http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx (accessed 27 March 2015)

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O’Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H (2013) vegan: Community Ecology Package. http://CRAN.R-project.org/package=vegan

Potts SG, Willmer P (1997) Abiotic and biotic factors influencing nest-site selection by Halictus rubicundus, a ground-nesting halictine bee. Ecological Entomology 22:319-328

Potts SG, Vulliamy B, Roberts S, O'Toole C, Dafni A, Ne'eman G, Willmer P (2005) Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecological Entomology 30:78-85

Pulliam HR (1988) Sources, Sinks and Population Regulation. American Naturalist 132: 652-661

Roulston TAH, Goodell K (2011) The role of resources and risks in regulating wild bee populations. Annual Review of Entomology 56:293-312

Sardiñas HS, Kremen C (2014) Evaluating nesting microhabitat for ground-nesting bees using emergence traps. Basic and Applied Ecology 15:161-168

Sardiñas HS, Kremen C (2015) Pollination services from field-scale agricultural diversification may be context-dependent. Agriculture, Ecosystems & Environment 207:17-25

Sardiñas HS, Tom K, Ponisio LC, Rominger A, Kremen C (2015) Sunflower (Helianthus annuus) pollination in California's Central Valley is limited by native bee nest site location. Ecological Applications (in press)

Stephen, WP (1960) Artificial Bee Beds for the Propagation of the Alkali Bee, Nomia melander. Journal of Economic Entomology 53:1025-1030.

Ullmann KU (2015) The role of connectivity and disturbance in dynamic landscapes: Squash bees (Peponapis pruinosa) in Yolo County, California. Doctoral dissertation. ProQuest Dissertations and Theses ID 15002

Westrich P (1996) Habitat requirements of central European bees and the problems of partial habitats. In Linnean Society Symposium Series 18:1-16. Academic Press Limited.

Wilkerson ML (2014) Using hedgerows as model linkages to examine non-native plant patterns. Agriculture, Ecosystems & Environment 192:38-46

Winfree R (2010) The conservation and restoration of wild bees. Annals of the New York Academy of Sciences 1195:169-197

Wratten SD, Gillespie M, Decourtye D, Mader E, Desneux N (2012) Pollinator habitat enhancement: benefits to other ecosystem services. Agriculture, Ecosystems & Environment 159: 112-122

Wuellner CT (1999) Nest site preference and success in a gregarious, ground-nesting bee Dieunomia triangulifera. Ecological Entomology 24:471-479

Xie Z, Qiu J, Chen X (2013) Decline of nest site availability and nest density of underground bees along a distance gradient from human settlements. Entomological Science 16:170-178

Zurbuchen A, Landert L, Klaiber J, Müller A, Hein S, Dorn S (2010) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biological Conservation 143:669-676

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Springer.

Figures

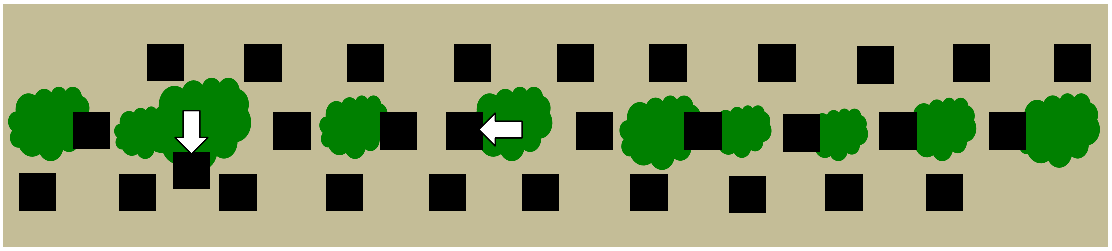


Fig. 1. Sampling scheme for 30 emergence traps (black boxes) to capture ground-nesting bees in field edges with and without hedgerow plantings. If a hedgerow shrub (green) was in the location where an emergence trap was to be placed, we first tried to put the trap in line with the hedgerow, next to the shrub (left-pointing arrow); however, if another shrub was adjacent to the first, we then put the trap to another side (downward pointing arrow). In both cases we placed the trap as close to the shrub as possible.

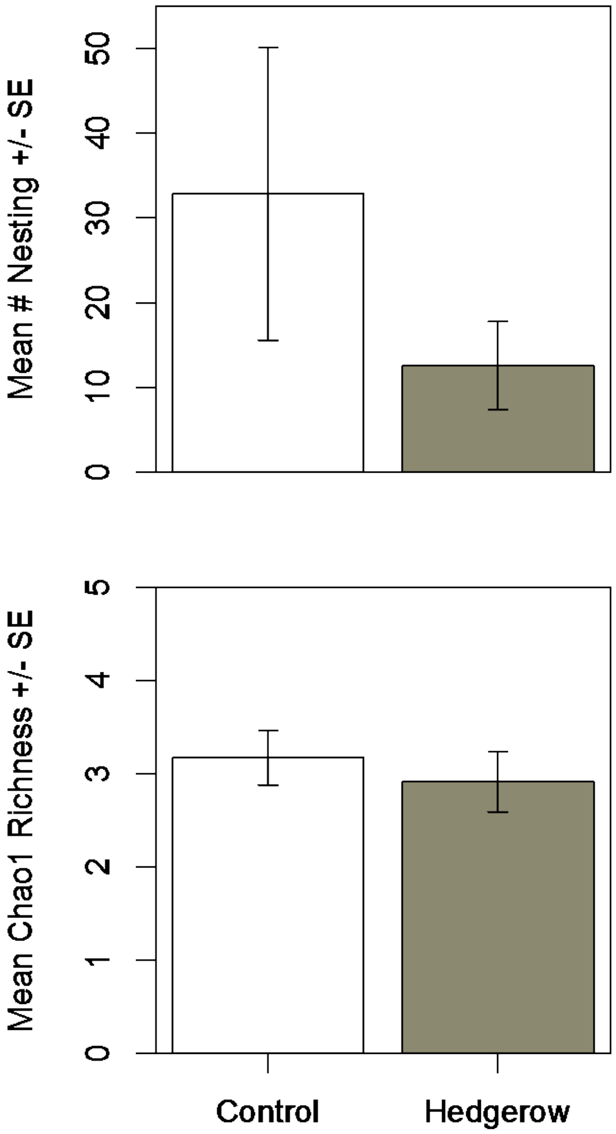


Fig. 2. Mean (± SE) bee abundance per site and Chao1 (abundance-based) species richness of ground-nesting bees collected in emergence traps in hedgerow and control field edges.

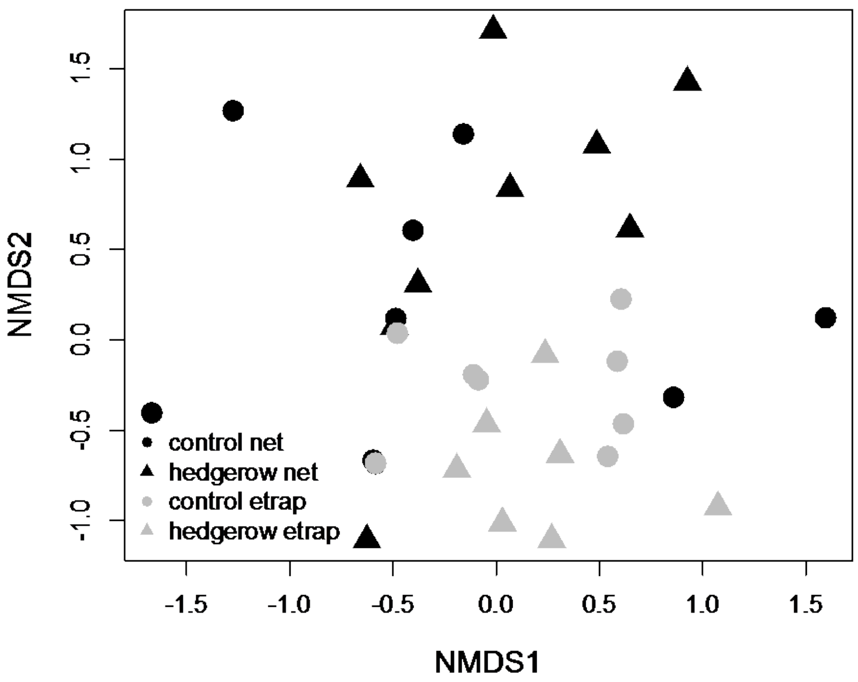


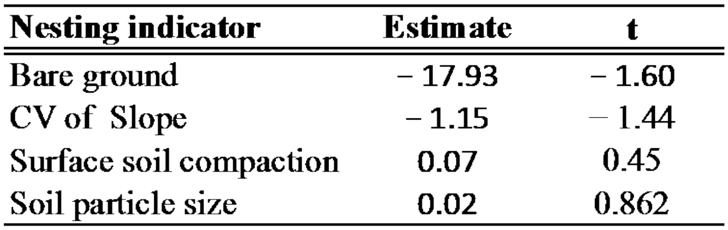
Fig. 3. Chao dissimilarities between ground-nesting bee assemblages nesting and foraging in hedgerow and control edges visualized using non-metric dimensional scaling (NMDS). Communities of foraging (aerial net) versus nesting (e-traps) of ground-nesting bees are distinct.

Tables

Table 1. Nesting indicators used to characterize nesting habitat within emergence traps. We focused on nesting indicators that had previously been found to affect ground-nesting bee nesting rates significantly (Wuellner 1999; Potts et al. 2005; Sardiñas and Kremen, 2014; Sardiñas et al. 2015). All indicators were measured at the trap-level except soil particle size, which was assessed at the site-level.

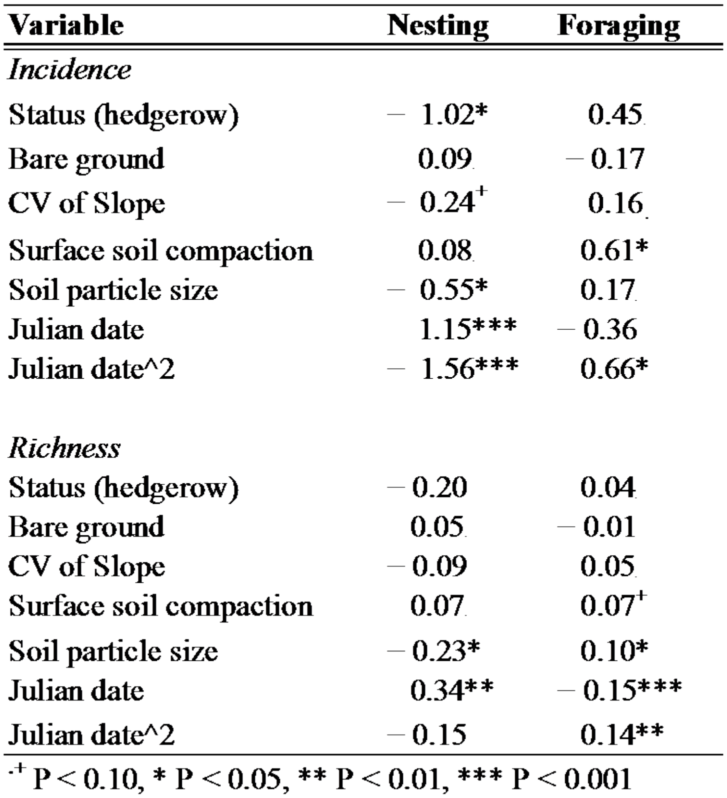
Nesting indicator	**Measurement**
Bare ground	% bare exposed soil
Slope variability (Proxy for soil surface irregularity)	We took 3 measurements of slope in each e-trap: 2 in corners and 1 in the center using a pitch and slope locator (Model No. 700, Johnson Level & Tool Mfg. Co., Mequon, WI, USA)
Surface soil compaction	We took 3 measurements of surface resistance (range 0- 4.5 kgf cm^2) with a penetrometer (Model no. 77114, Forestry Suppliers, Inc., Jackson, MS, USA)
Soil particle size	Average particle size (microns) from a 5g sample processed in a laser diffraction particle size analyzer (Sequoia LISST Portable XLR)

Table 2. Effect of hedgerow presence on nesting indicators. The estimate provides the effect size of the nesting indicator in hedgerow sites, when compared to unenhanced, control field edges. All results were non-significant.



Nesting indicator	**Estimate**	**t**
Bare ground	− 17.93	− 1.60
CV of Slope	− 1.15	− 1.44
Surface soil compaction	0.07	0.45
Soil particle size	0.02	0.862

Table 3. Model results of the influence of site status (hedgerow present or absent) and indicators of nesting quality on the abundance and rarefied richness (Chao-1) of ground-nesting bees found in emergence traps (Nesting) and netted on inflorescences in hedgerow or control sites (Foraging).



Variable	Nesting	Foraging
Incidence		
Status (hedgerow)	− 1.02*	0.45
Bare ground	0.09	− 0.17
CV of Slope	− 0.24^{+}	0.16
Surface soil compaction	0.08	0.61*
Soil particle size	− 0.55*	0.17
Julian date	1.15***	− 0.36
Julian date^2	− 1.56***	0.66*
Richness		
Status (hedgerow)	− 0.20	0.04
Bare ground	0.05	− 0.01
CV of Slope	− 0.09	0.05
Surface soil compaction	0.07	0.07^{+}
Soil particle size	− 0.23*	0.10*
Julian date	0.34**	− 0.15***
Julian date^2	− 0.15	0.14**

$^{+}$ P < 0.10, * P < 0.05, ** P < 0.01, *** P < 0.001

Supplement

Figure S1. Hedgerow (red) and control (yellow) field edges in our study landscape, Yolo County, in the CA Central Valley.

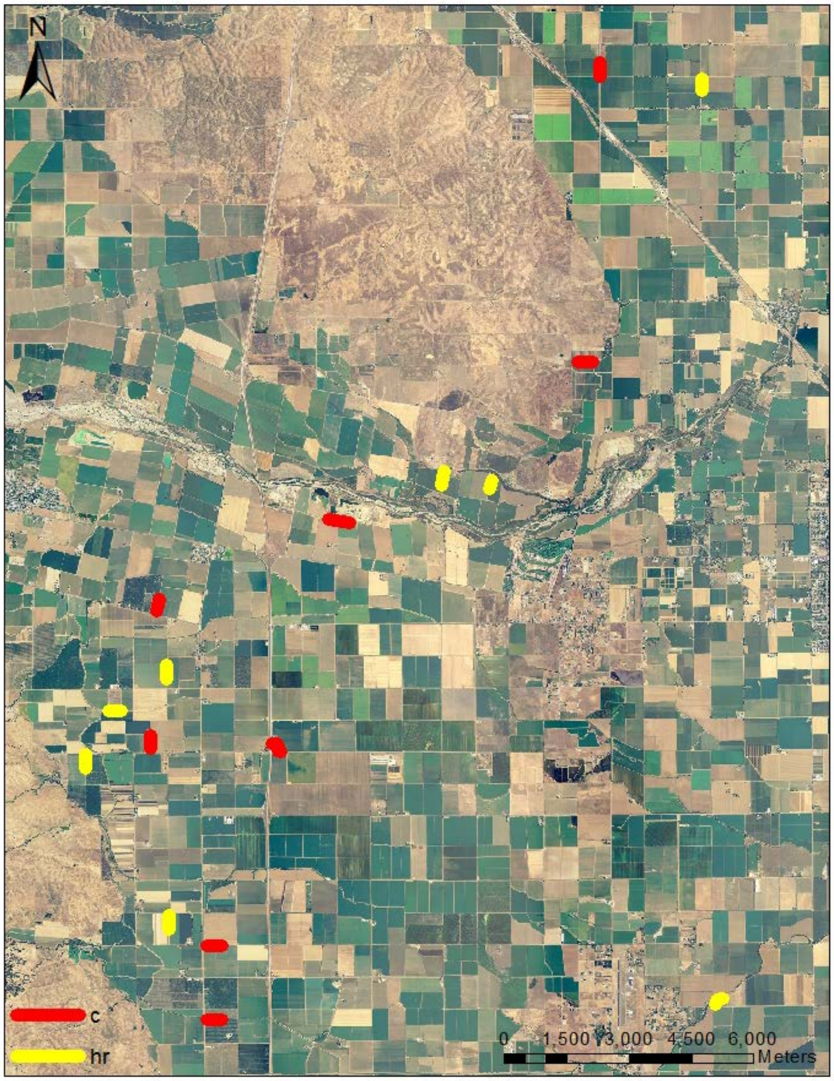


Figure S2. Rarefaction curves of species collected in emergence traps (e-trap) in hedgerow and control sites over 3 sample rounds. We placed 30 e-traps per site per sampling round.

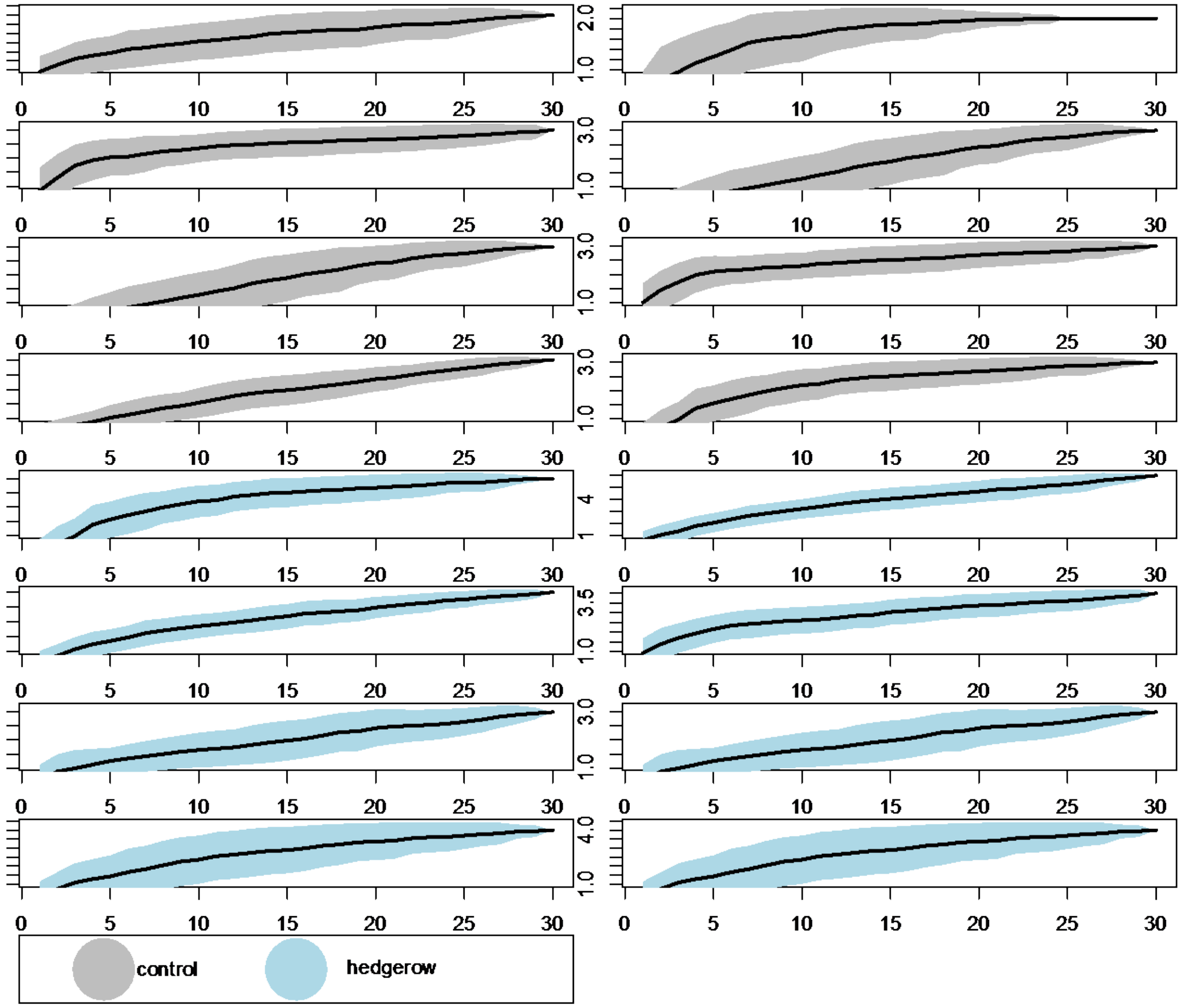


Figure S3. Histograms of site characteristics we measured as indicators of nesting habitat quality.

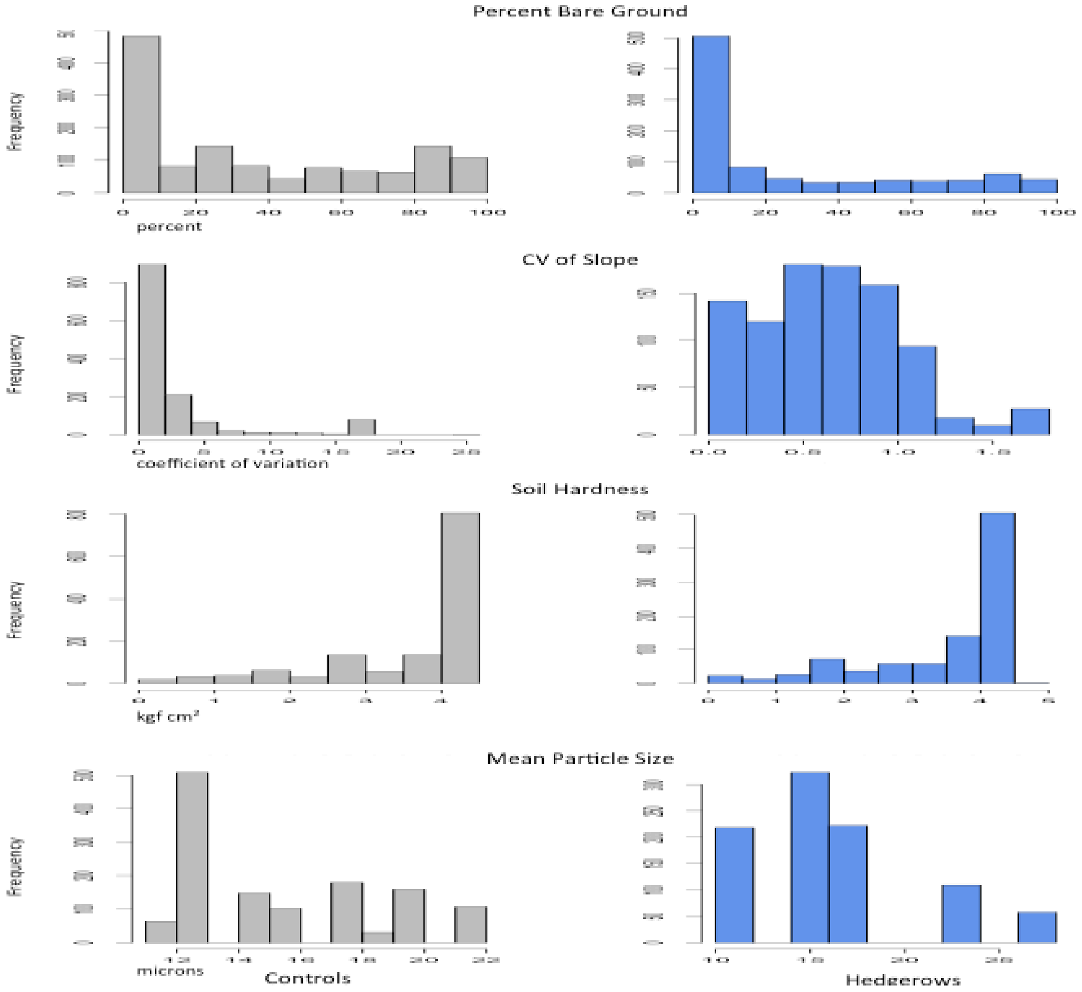
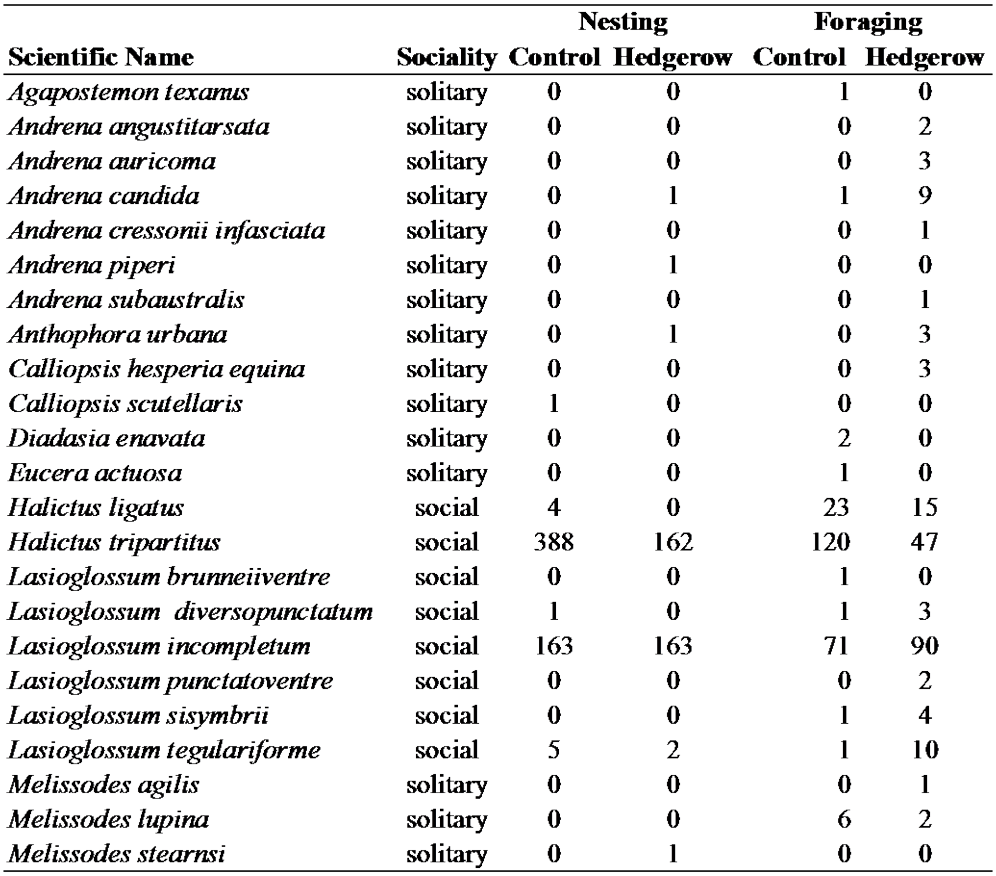


Table S1. Plant species flowering in hedgerow only (H), control only (C), and both site types during e-trap sampling. Hedgerows contained native perennial forbs and shrubs that were intentionally planted to supply pollen and nectar for pollinators. Hedgerows also contained numerous weedy, unplanned species; the majority of weedy species found in hedgerows were also found in control sites (unmanaged field edges).

	Scientific name	**Habit**	**Native**	**Sites present**
Intentionally Planted	*Achillea millefolium*	perennial forb	native	H
	Aster chilensis	perennial forb	native	H
	Atriplex triangularis	shrub	native	B
	Baccharis salicifolia	shrub	native	H
	Ceanothus sp.	shrub	native	H
	Epilobium campestre	annual forb	native	H
	Eriogonum fasiculatum	shrub	native	H
	Eschscholzia californica	annual forb	native	H
	Fremontia californica	shrub	native	H
	Grindelia camporum	perennial forb	native	H
	Heliotropium curassavicum	perennial forb	native	H
	Heteromeles arbutifolia	shrub	native	H
	Lavendula officinalis	shrub	native	H
	Prunus ilicifolia	shrub	native	H
	Rhamnus tomentella	shrub	native	H
	Rosa californica	shrub	native	H
	Salvia clevelandii	shrub	native	H
	Sambucus mexicana	shrub	native	H
Unplanned Species	*Anthemis cotula*	annual forb	non-native	H
	Brassica sp.	annual forb	non-native	B
	Carduus pycnocephalus	annual forb	non-native	B
	Capsella bursa-pastoris	annual forb	non-native	C
	Centaurea solstitialis	annual forb	non-native	C
	Convolvulus arevensis	annual forb	non-native	B
	Conyza canidensis	annual forb	non-native	C
	Croton setigerus	annual forb	native	C
	Erodium cicutarium	annual forb	non-native	B
	Latuca serriola	annual forb	non-native	C
	Lepidium latifolium	perennial forb	non-native	C
	Lotus corniculatus	perennial forb	non-native	C
	Malva neglecta	annual forb	non-native	B
	Marrubium vulgare	perennial forb	non-native	B
	Medicago polymorpha	annual forb	non-native	H
	Picris echioides	annual forb	non-native	B
	Polygonum arenastrum	annual forb	non-native	B
	Raphanus raphanistrum	annual forb	non-native	C
	Silybum marianum	annual forb	non-native	B
	Sonchus asper	annual forb	non-native	H

Table S2. Bee species collected from emergence traps (nesting species) and from inflorescences in hedgerow and control sites (foraging species). Solitary bees nest one female bee per nest whereas social bees usually have more than one bee per nest.



		Nesting		Foraging	
Scientific Name	**Sociality**	**Control**	**Hedgerow**	**Control**	**Hedgerow**
Agapostemon texanus	solitary	0	0	1	0
Andrena angustitarsata	solitary	0	0	0	2
Andrena auricoma	solitary	0	0	0	3
Andrena candida	solitary	0	1	1	9
Andrena cressonii infasciata	solitary	0	0	0	1
Andrena piperi	solitary	0	1	0	0
Andrena subaustralis	solitary	0	0	0	1
Anthophora urbana	solitary	0	1	0	3
Calliopsis hesperia equina	solitary	0	0	0	3
Calliopsis scutellaris	solitary	1	0	0	0
Diadasia enavata	solitary	0	0	2	0
Eucera actuosa	solitary	0	0	1	0
Halictus ligatus	social	4	0	23	15
Halictus tripartitus	social	388	162	120	47
Lasioglossum brunneiiventre	social	0	0	1	0
Lasioglossum diversopunctatum	social	1	0	1	3
Lasioglossum incompletum	social	163	163	71	90
Lasioglossum punctatoventre	social	0	0	0	2
Lasioglossum sisymbrii	social	0	0	1	4
Lasioglossum tegulariforme	social	5	2	1	10
Melissodes agilis	solitary	0	0	0	1
Melissodes lupina	solitary	0	0	6	2
Melissodes stearnsi	solitary	0	1	0	0

The difference in nesting resources between hedgerows and unmanaged field margins did not positively impact wild bee nesting. Bees may therefore be nesting in other areas of the landscape, including natural habitat and crop fields, and foraging into hedgerow to utilize the floral resources they provide. Current models of pollination services in agricultural landscapes do not reflect the patterns of nesting I observed in hedgerows, instead they categorize hedgerows and other edge habitat as having high nesting quality. The model parameterizations are based on expert opinion and not on empirical data of nest site locations. The next chapter tests pollination model parameterizations.

Pollination models are useful because they help growers identify areas that are likely receiving sufficient pollination from wild bees, and areas that might have pollen deficits, requiring habitat restoration or increased honey bee abundance obtainable through hive rental. If these models are incorrectly incorporating the distribution of wild bees, which they extrapolate from data on floral abundance and suitable nesting locations, then the information utilized by growers may be erroneous. We examine not only where bees are nesting, but also whether local-scale floral resources impact wild bee populations. In addition, because bees have limited foraging ranges around their nest locations, we measure foraging distance using luminous powder to determine whether predictions based on body size are accurate. We then combine these three metrics (forage, nests and flight range) to predict the pollination coverage within a single crop field, the unit of measurement of greatest interest to the farmer.

Chapter 4

Sunflower (*Helianthus annuus*) pollination in California's Central Valley is limited by native bee nest site location

Hillary S. Sardiñas, Kathleen Tom, Lauren Catherine Ponisio,
Andrew Rominger, and Claire Kremen

Accepted for Publication in
Ecological Applications
June 2015

Abstract

The delivery of ecosystem services by mobile organisms depends on the distribution of those organisms which is, in turn, affected by resources at local and landscape scales. Pollinator-dependent crops rely on mobile animals like bees for crop production, and the spatial relationship between floral resources and nest location for these central-place foragers influences the delivery of pollination services. Current models that map pollination coverage in agricultural regions utilize landscape-level estimates of floral availability and nesting incidence inferred from expert opinion, rather than direct assessments. Foraging distance is often derived from proxies of bee body size, rather than direct measurements of foraging that account for behavioral responses to floral resource type and distribution. The lack of direct measurements of nesting incidence and foraging distances may lead to inaccurate mapping of pollination services. We examined the role of local-scale floral resource presence from hedgerow plantings on nest incidence of ground-nesting bees in field margins and within monoculture, conventionally managed sunflower fields in California's Central Valley. We tracked bee movement into fields using fluorescent powder. We then used these data to simulate the distribution of pollination services within a crop field. Contrary to expert opinion, we found that ground-nesting native bees nested both in fields and edges, though nesting rates declined with distance into field. Further, we detected no effect of field-margin floral enhancements on nesting. We found evidence of an exponential decay rate of bee movement into fields, indicating that foraging predominantly occurred in less than 1% of medium-sized bees' predicted typical foraging range. Although we found native bees nesting within agricultural fields, their restricted foraging movements likely centralize pollination near nest sites. Our data thus predict a heterogeneous distribution of pollination services within sunflower fields, with edges receiving higher coverage than field centers. To generate more accurate maps of services we advocate directly measuring the autecology of ecosystem service providers, which vary by crop system, pollinator species and region. Improving estimates of the factors affecting pollinator populations can increase the accuracy of pollination service maps and help clarify the influence of farming practices on wild bees occurring in agricultural landscapes.

Keywords

Agriculture; Bee conservation; Ecosystem service provider; Floral enhancements; Fluorescent dye; Foraging; Hedgerows; Mass-flowering crops; Mobile agent-based ecosystem services; Nesting.

Introduction

For ecosystem services provisioned by mobile organisms, the distribution and foraging range of ecosystem service providers impacts the stability and magnitude of services delivered (Kremen et al. 2007, Garibaldi et al. 2011, Jonsson et al. 2014). Resource availability at local and landscape scales is a key driver of the abundance and richness of species that provide ecosystem services (Kremen 2005). Quantifying the spatial distribution of key resources can help map ecosystem services; however, predictions of service provisioning depend on the accuracy of resource assessments. At the landscape-scale, proxies are often used to describe resource distributions. For example, in models of pollination services, proxies have been developed for each of the three main factors that influence the distribution of native bees and hence their ability to pollinate crops. Currently, land cover is used as a proxy for floral richness or abundance (Lonsdorf et al. 2009, Ricketts and Lonsdorf 2013, Schulp et al. 2014), nesting habitat quality is a proxy for nesting rates (Keitt 2009, Lonsdorf et al. 2009), and bee body size is a proxy for foraging range (Benjamin et al. 2014, Lonsdorf et al. 2009). However, if such proxies poorly capture floral resources, nesting habitat quality and foraging ranges, then maps of predicted pollinator abundances or services may not reflect actual levels of pollination provided to crops. In this paper, we make direct measurements of these parameters in order to map pollination services at the scale of a farm field.

The data used to map floral resources in current pollination models is often at large spatial scales derived from remotely-sensed data. This approach can miss finer-scale patterns in vegetation that may affect bee foraging patterns, and therefore potentially under- or over-estimate pollination services (Lonsdorf et al. 2009). Local floral resources can have strong effects on native bee communities (Potts et al. 2003, Roulston and Goodell 2011, Williams and Winfree 2013). Responses to increased floral diversity at the field-scale, through crop diversification or field-margin floral enhancements, include heightened native bee abundance within field edges and in crop fields (M'Gonigle et al. *in press*, Morandin and Kremen 2013). However, because bees are mobile and are central-place foragers, both the location of their nest sites and their foraging range can mediate the effects of floral resources. For example, specialist bees may prefer to nest in close proximity to their host plants, as exemplified by the squash specialist *Peponapis pruinosa*, which nests at higher rates within squash fields (Esther Julier and Roulston 2009). Similarly, adding floral resources to field margins could increase the attractiveness of these locations as nest sites.

It is challenging to quantify nesting incidence because nests are difficult to locate (Sardiñas and Kremen 2014); therefore, within pollination models, nesting is predominantly based on expert opinion rather than nesting surveys. By using expert opinion, however, the areas predicted to support native bee ground-nesting is limited to field edges and natural habitats (Brosi et al. 2008, Lonsdorf et al. 2009, Rands & Whitney 2011). Brosi et al. (2008)'s model, which optimizes pollination services in agricultural landscapes, divided the farmscape into natural habitat cells or agricultural cells; nesting was restricted to the natural habitat cells. The rationale for limiting nesting to specific areas is based on the assumption that bees prefer undisturbed soils, such as untilled field margins and remnant natural habitat (Chaplin-Kramer et al. 2011; Rands and Whitney 2011). Agricultural fields are therefore presumed to contain fewer nests than semi-natural habitats due to farm management practices including irrigation and tillage. There is conflicting evidence, however, concerning the effects of soil disturbance on below-ground nesting. A meta-analysis found that the relative abundance of below-ground nesting bees increased in disturbed habitats, although tilling had an overall negative effect, with the strength of the effect varying by species (Williams et al. 2010). Both generalist and specialist species have been found nesting directly within tilled sunflower fields, although nesting rates in undisturbed field margins were higher than within fields (Kim et al. 2006). The ability of bees to nest in agricultural fields calls into question the rationale for limiting nesting to field margins or non-crop areas within agricultural landscapes; relaxing this constraint could dramatically alter current model predictions.

The pollination maps produced by these models provide tools that could potentially influence on-farm land use decisions. Maps that highlight the importance of habitat features for augmenting pollinator abundances, such as proximity to field-scale diversification techniques, could enhance grower adoption of conservation practices (Stonehouse 1996, Knowler and Bradshaw 2007). Such maps and models could also affect the promotion of on-farm diversification techniques by government programs, such as the Environmental Quality Incentive Program in the United States and agri-environmental schemes in Europe (Vaughan and Skinner 2008). Improving estimates of the factors affecting pollinator populations can increase the accuracy of pollination service maps and help clarify the influence of farming practices on wild bees occurring in agricultural landscapes.

To facilitate development of models based on measurements of nesting and foraging inputs rather than expert opinion or proxies, we examined the nest location and movement of ground-nesting bees in intensively managed mass-flowering crop fields with or without local floral resource enhancements provided by bordering hedgerows. In accordance with previously published model parameterizations, we predicted that (i) native bees would only nest in edges, and that (ii) field margins containing the floral enhancements provided by hedgerows would provide better nesting habitat than unenhanced field margins. We also expected to (iii) find evidence that within crop fields, bee foraging distances are consistent with allometric predictions of their typical foraging range. We then use these data to model the coverage of pollination services within a single crop field.

Materials and Methods

Study system

This study was conducted in sunflower (*Helianthus annuus*) fields in Yolo Co., in California's Central Valley from June to July in 2012 and 2013 (Fig. A1). To maintain independence between fields, we ensured fields were a minimum of 900 m apart (range, 947-5,409; Greenleaf et al. 2007). Sunflower is an artificially gynodioecious pollinator-dependent row crop with male-sterile (female) heads that produce nectar and male-fertile (male) heads that produce both nectar and pollen (Greenleaf and Kremen 2006). There is one male row for every 4-6 female rows. To facilitate isolation of hybrid offspring, sunflower fields are moved each year; therefore none of the fields were sampled in both years.

Floral resources

To evaluate whether local-scale floral resources influenced native bee nesting, we sampled sunflower fields adjacent to either hedgerows or unenhanced field margins (hereafter "controls"). Hedgerows contained native flowering shrubs and forbs that bloom sequentially over the year to provide resources to bee species with differing flight periods (Long and Anderson 2010). Each hedgerow was between 250-300 m in length. Control sites were bare or weedy field margins. When we sampled a sunflower field adjacent to a hedgerow, we also sampled a control field containing the same sunflower variety, at the same stage of bloom (> 90% of heads flowering), and in the same landscape context (similar proportion of natural habitat within a 1 km buffer) within one week.

We collected data on floral cover and diversity in each site in the same quadrats in which we sampled nesting (see Nesting section below). Only a portion of the plant species present within the hedgerows bloomed during our study period (Table A1). Hedgerows also contained weedy species; the most predominant were *Convolvulus arvensis* (bindweed), *Brassica* spp. (wild mustard), and *Polygonum arenastrum* (common knotweed). Hedgerow composition and history are described in detail in Long et al. (1998). Controls sites did not contain any native plant species (Table A1); dominant weedy species were the same as those in hedgerows.

Nesting

We examined ground-nesting rates in ten sunflower fields in 2012 and eight fields in 2013 (Fig.S1). We set ten 0.6 m^2 emergence traps (e-traps; Bug Dorm, Taichung, Taiwan) spaced 20 m apart along a single transect in field margins with and without hedgerows (Fig. 1). We then placed five e-traps at 0, 10, 50, 100 and 200 m along each of two 200 m parallel transects (T1 and T2) extending into each field (Fig. 1). Each e-trap was equipped with a kill jar at its apex filled one-third full with soapy water. The edges of the e-traps were secured with soil to prevent any bees from entering or exiting. We placed traps at dusk, after bees had retired to their nests, thus any bees collected in the e-traps were those emerging from their nests to forage. We emptied the kill jars approximately 20-22 hours after traps were set. We stored all specimens in 95% ethanol until they were pinned, after which they were identified by expert taxonomist Dr. Robbin Thorp (Professor Emeritus, Harry H. Laidlaw Jr. Honey Bee Research Facility, University of California, Davis), and stored in the Essig Museum at UC Berkeley. Only female bees are considered in analyses as male bees may have been resting in vegetation and are not indicative of nesting rates (Kim et al. 2006).

Soil characteristics may influence nesting incidence and potentially provide a proxy for nesting habitat suitability in pollination models. Therefore we measured mean particle size and soil heterogeneity. We collected four soil samples at 10 cm depth at each site, two along a transect in the field margins at 40 and 60 m, and two in each field at 10 m on T1 and 100 m on T2. Soil was then dried in a forced air oven at 40°C for two days and sieved to remove coarse particles (> 2mm). We calculated average particle size with a laser diffraction particle size analyzer (Sequoia LISST Portable XLR). To measure soil heterogeneity within a 1 km buffer around each site, we calculated Shannon's diversity index, the proportional abundance of each soil class. Soil classes were identified from the 2013 Natural Resource Conservation Service soil map (U.S. Department of Agriculture 2013).

Key habitat features that might influence nesting have also been examined as proxies for nesting (Table A2; Sardiñas and Kremen, 2014, Potts et al. 2005). We therefore visually estimated percent bare ground, percent vegetative cover, percent leaf litter, percent rocks, dead wood, cracks, cavities, slope of the ground, and surface soil compaction within each e-trap (hereafter "nesting characteristics").

Foraging

We tracked bee movement in a subset of eight sunflower fields in 2012. In each field we delineated six or seven 100 m transects (depending on row spacing within the field) in each male row between 0-50 m from the field edge (Fig. 1), measuring the distance between each transect. We walked the along the first collecting medium-sized male and female bees with nets and bug vacuums (Backyard SafariTM). We defined medium-sized bees to be approximately the size of the European honey bee *Apis mellifera*. In our study system this included the genera *Diadasia*, *Melissodes*, *Megachile*, *Pepopnapis*, and *Triepeolus*. Each bee was placed in a collecting vial containing fluorescent powder (Shannon Luminous Materials, Inc., Santa Ana, CA, USA; Frankie 1973, Stockhouse 1976). The vibration of the bees' wings caused the powder to disperse throughout the vial, coating each bee completely. Bees were released after approximately five seconds. The majority of bees then departed the transect, exhibiting a typical stress response. They were typically not seen again during collection, which lasted 2-5 hours depending on the site. We attempted to standardize the number of bees marked to 100 bees per site, but in some cases were unable to collect the full number (range, 70-120). To standardize environmental factors that could affect foraging, we began collection at 9 am at each site and only sampled when weather conditions were clear/sunny, wind speeds were below 2.5 m/s, and temperatures were above 18°C.

To quantify the marks left by bees in the field, 2 people walked each transect for 30 minutes after dusk scanning both male and female sunflower heads with UV lights for traces of luminous powder. We also searched within field margins, but did not find a single mark over the course of the study. The fact that we found marks close to release sites indicates that bees did return to the places they were originally caught. In fact, we noted dyed bees entering their nest holes in the rows where they were marked (H.S.S., pers. obs.).

Normal bee behavior, such as grooming and flight, could result in powder loss. Over a four hour period, bumble bees were found to lose approximately 6.1% of the pollen (or powder) collected on their body in ways unrelated to pollination, such as flight, grooming, or landing on other parts of the (Rademaker et al. 1997). To determine whether the amount of powder observed was affected by the physical loss of powder through activities other than pollination, we evaluated the number of powder depositions that a single marked bee is able to make by coating dead *Melissodes* specimens with luminous powder and pressing them onto sunflowers in the lab (Rademaker et al. 1997). We found specimens were still able to deposit dye after 20 presses. Many fewer than 20 powder observations per marked bee were found in the field, indicating that declines in observation with distance into the field were not solely a result of unrelated powder loss.

Analyses

We standardized all nesting characteristics (subtracted mean and divided by standard deviation), then checked them for collinearity. Because of strong negative correlation with percent bare ground, we removed percent leaf litter and vegetation, but retained all other nesting variables.

We analyzed nesting abundance using a negative binomial model in the R package lme4 (Bates et al. 2014). Although the bee nesting data contained a high number of zeros, we did not find evidence of overdispersion. However, negative binomial models are prone to high type I error rates (Ives 2015); we therefore used model validation procedures to test our abundance model for this issue (Appendix B). Fixed effects were distance into field, hedgerow presence (hedgerow or control edge), soil particle size, soil heterogeneity, and nesting characteristics. We also included an interaction between distance into field and hedgerow presence to determine whether hedgerows impacted nesting rates within fields. Site was included as a random effect. We evaluated variables using a stepwise process and comparing AIC scores (scores with 4 AIC points were considered comparable). The nesting characteristics percent rocks, wood, cracks and cavities were eliminated in this manner.

We assessed nesting incidence, coded as presence or absence (1, 0), using the same fixed and random effects as in the abundance model but with a generalized linear mixed model with a binomial distribution in the R package MASS (Venables and Ripley 2002). We analyzed raw species richness using a generalized linear mixed model in the R package nlme (Pinheiro et al. 2015). We then visually compared rarefied richness by site in fields and edges with and without hedgerows using 100 permutations of the random species accumulation method in vegan (Oksanen et al. 2013). To estimate total species richness across all sites we used a jackknife from the vegan package (Oksanen et al. 2013).

To determine the rate of decay of powder marks we used a non-linear least square regression. We then assessed the effects of the number of bees marked in each site, the ratio of female to male bees marked, distance from the marked row (shortest linear distance from “mark” row to “recapture” row), and treatment (hedgerow versus control field) on the number of powder observations using a generalized linear mixed model with a Poisson distribution with row nested within site as a random factor in the R package lme4 (Bates et al. 2014, Zuur et al. 2009).

Mapping

To map pollination coverage in a single hybrid sunflower field, we first simulated the distribution of nests. In the nesting data we found that nests were well described by a negative binomial distribution. To approximate this distribution, we used a log Gaussian Cox process (Cox and Isham 1980). The log Gaussian Cox process models nest density as a spatially explicit log-Gaussian surface and then generates exact nest locations by sampling the surface with a Poisson process. An advantage of this approach is that the Gaussian surface captures potential spatial co-variance in nest density. Using the R package spectralGP (Paciorek 2007), we parameterized the Gaussian process with an exponential covariance structure and a mean density of 0.1 nests per meter, reflecting the average number of observed nests per site. We also included a mild edge effect, allowing the mean density to increase exponentially by 5% toward the edge of the field. We computed the log of this distribution, used this spatially varying surface as the density of nests, generating exact nest locations via a Poisson process using the R package spatstat (Baddeley and Turner 2005). Next, we approximated bee foraging ranges from these nests with an exponential decay rate of 1, approximately what we found in our movement study and also the decay rate utilized in the Lonsdorf pollination services model (Lonsdorf et al. 2009). The resulting incidence of bee nests within a field combined with the foraging range around those nests depicts the expected pollination coverage from medium-sized bees predicted by our data.

Results

We collected 95 female ground-nesting bees from e-traps representing 10 species (Table A3). Our total jackknifed species richness across all sites and years was 15 ± 3. We did not find a higher number of species in hedgerows or fields adjacent to hedgerows. However, when we rarefied richness separately for field borders and fields both with and without hedgerows, we found that the number of nesting species accumulated continued to increase, particularly in control margins that lacked hedgerows (Fig. A2).

Nesting in agricultural edges and fields

Ground-nesting bees nested in both field margins and within sunflower fields; however, we found higher numbers of bees nesting in margins than within fields ($t = 9.263$, $P < 0.01$; Table 1; Fig. 2). Within fields, nests were clustered near the field borders, though we found lower densities of nests throughout fields (Fig. 2). The richness of nesting species was also slightly higher in margins ($t = -1.92$, $P = 0.056$). Hedgerow presence did not influence the abundance ($t = -0.143$, $P = 0.733$), incidence ($t = -0.51$, $P = 0.621$), or richness ($t = -0.88$, $P = 0.392$) of ground nesters. Nesting was associated with areas containing steeper slopes, but not with soil hardness (Table 1).

All soils from our study sites were classified as clay loams (Fig. A3). Soils from field margins and within fields at the same site were more similar to one another than fields were to other fields and edges were to other edges. We did not detect an effect of soil particle size on nesting however, we did find a marginally significant trend of increased nesting with higher soil heterogeneity in the surrounding landscape (Table 1).

Patterns of movement detected

We dyed a total of 743 medium-sized bees with luminous powder, with a median of 101 per site. 72.4% of all bees dyed were in the genus *Melissodes*, with 428 females and 110 males (Table A3). 97.2% were sunflower specialists (Table A3). We observed 464 traces of powder on sunflower heads, with 80.7% concentrated in the first row. Powder marks decayed at a rate of 0.9964 ($t = 2.80$, $P = 0.009$) from the transect in which bees were marked (Fig. 3). Distance into the field had the strongest effect on the dye marks observed ($z = -6.50$, $P < 0.001$; Table 2). Hedgerow presence did not impact bee movement ($z = 0.47$, $P = 0.64$), nor did it interact with distance ($z = 0.42$, $P = 0.67$). We did observe more dye traces in fields where more bees were marked ($z = 2.47$, $P < 0.05$), but the sex of the bee did not influence the pattern of dye deposition ($z = 0.35$, $P = 0.73$).

Mapping services in a single field

Using the nesting rates and foraging distances we observed, we predict a spatially heterogeneous pattern of ecosystem service delivery within a single crop field (Fig. 4). The rapid decline in dye marks we observed indicates a truncated foraging range, likely centralized around nest location. Thus, the distribution and density of nests (Fig. A4) within a given field could influence foraging extent. In our e-trap sampling, we found higher numbers of nests in edges and within the first 10 m into crop fields. We would thus predict pollination services to be spatially clustered around these nests sites, and therefore higher along field edges than centers.

Discussion

Assessing model parameterizations

Contrary to our expectations, our findings did not support our specific predictions, nor did they support many of parameterizations typically used in pollination service models. First, we detected nests in both fields and field margins; however, we did find higher nesting rates in areas bordering fields. Second, we did not find that hedgerow plantings increased nesting rates. Third, the majority of bee foraging activity we detected occurred within a fraction of the predicted foraging range of the dominant genus, instead of throughout its foraging range, indicating that utilizing an exponential decay function for foraging range is critical to capturing the distances covered by native bees in pollination service models (e.g., as in the Lonsdorf et al. model). Some of the differences between these results and the expert opinions upon which pollination service models are currently based could result from factors associated with mass-flowering crops. Nevertheless, we cannot compare whether the trends we observed are particular to a mass-flowering crop system because nesting and foraging patterns have not been examined across different crop systems and regions. Thus, the divergence of our results from expert opinion strongly argues for testing expert opinion with field experiments. In addition, our findings indicate that pollination coverage in mass-flowering crop fields is likely limited by bee nest site location. Factors that affect nesting, including farm management techniques as well as soil conditions and nesting characteristics therefore require further attention in order to improve pollination service delivery at the farm scale.

Nest location and nesting resources

Our findings confirm that native bees nest in fields despite management practices that cause disturbance, although only a portion of their offspring may survive soil disturbance events (Ullmann 2015). Thus, parameterizations that limit nest site location to edge habitat, such as in the Rands and Whitney (2011) model, may not capture realistic nest distributions. A parameterization that allows bees to nest within fields, though in greater numbers along edges (modeling an edge effect), would more realistically reflect the conditions in our study system. Crop-specific pollination coverage estimates resulting from direct measurements of nesting and foraging could be used to alter the size of crop fields to maximize pollination by wild bees. The ability to nest within fields not only benefits crop pollination, but may also contribute to the sustainability of pollinator populations over time. When Keitt (2009) modeled native bee persistence in agricultural landscapes, he found that allowing bees to nest in a variety of land use types within agricultural areas promoted long-term population viability whereas constraining nest-site location to field margins and other undisturbed sites limited population growth.

Patterns of nesting, however, likely differ based on crop attractiveness, bloom density, and the attractiveness and width of field-margin plantings. Thus, the trends we observed may not be representative of other crop systems or different geographic regions, indicating a need for crop- and region-specific nesting assessments. Sunflower, for example, is visited by both generalist and specialist bees because its open blooms are easily accessed by a variety of pollinators (Parker 1981, Greenleaf and Kremen 2006). We found generalist species (e.g. *Lasioglossum (Dialictus)* spp.) nesting in both fields and edges, while sunflower specialists *M. agilis* and *M. lupina* only nested within sunflower fields. *Lasioglossum (Dialictus) incompletum* is hyper-abundant in agricultural landscapes, and known to be a generalist floral visitor. It may also be a generalist in the nesting conditions it is willing to accept. Conversely, sunflower specialists may prefer to nest in locations where sunflower is growing, although they have been found nesting in irrigation furrows adjacent to zucchini *Cucurbita pepo* plots near sunflower fields (Parker et al. 1981). Bees that are not dependent on sunflower may find nesting within fields a less attractive option.

Bees have diverse nesting habits and thus species likely exhibit a variety of preferences. Thus, having a variety of soil conditions ought to improve the diversity of nesting species. We did detect a marginally significant affect of soil diversity surrounding our study sites on the abundance and richness of ground-nesters. However, the majority of the soils in our study region, both in tilled agricultural fields and untilled margins, have high clay content (Fig. S3). Clay soils are generally considered unfavorable for nesting. Clay content has been found to decrease nesting rates, while sand and silt are more favorable because they increase drainage (Cane 1991). That both specialists and generalists were found nesting in conditions considered by bee biologists to be unfavorable suggests that expert opinion on nest site location may need revision.

Floral resources and foraging

Although we found bees nesting in crop fields, pollination coverage may be limited, if actual foraging distances are much smaller than potential foraging ranges. The majority of movements we detected were within 10 m of where bees were marked, despite the fact that marked individuals generally immediately left the field in which they were marked due to a stress response. Following their departure, they likely returned to the site of capture, and then returned to foraging. We hypothesize that this behavior indicated that they were captured near their nest sites. *M. agilis*, the most common species we collected, has an average foraging range prediction of 740 ± 250 m, based on its body size (Greenleaf and Kremen 2006). However, in the presence of abundant resources provided by a mass-flowering crop, we found the majority of foraging movement was concentrated in <1% of its potential range. With an exponential decay rate of 1, we would have expected to find a higher concentration of marks up to 75 m into fields. We curtailed searching for marks at 50 m because we did not see any between 50 - 100 m in the first two fields we surveyed. Additionally, we were unable to search the full circumference around the point of marking. We did search within hedgerows and edges adjacent to fields, never finding a single powder mark. This evidence suggests that while bees may be capable of foraging larger distances, their movement may be concentrated in certain areas, particularly when there are ample and highly attractive nearby resources.

Floral densities can affect foraging behavior (Hegland and Boeke 2006). In intensive agricultural landscapes, mass-flowering crops can provide hundreds of thousands of blooms per field (Williams et al. 2012). Honey bees, for example, have been documented to forage shorter distances when presented with higher density of blooms (Waddington 1980). Densities of sunflower in our field ranged from 1 - 17 per m^2 for female plants to 3 - 25 per m^2 for males, which often had 1 - 11 flower heads per stem. In the presence of such abundant resources, bees likely only needed to forage a short distance from their nest sites to obtain the pollen and nectar required for nest provisioning and their own alimentation. As mentioned, dyed bees returned to the site of capture, which was likely near their nest location. However, if bees nest in fields with sparse resources, which we did not study, we would then expect them to fly greater distances within their maximum foraging range to access available floral resources (Zurbuchen et al.

2010). Adding a measure of floral density to current models that alters expected foraging range predictions could help address this issue.

Spatial and temporal scales of mapping

Low resolution mapping of floral and nesting resources may capture general pollination trends within an agricultural region, but may not be informative to farmers who are interested in services within their crop fields. In the same study landscape where we conducted this study, Lonsdorf et al. (2009)'s model predicted that pollination coverage for watermelon would be very low, but relatively evenly distributed except where agricultural areas were adjacent to natural habitats, where pollination is predicted to be higher. Our visualization within a single sunflower field illustrates that pollination may be highly variable at the scale of interest to growers. Our finding supports Lonsdorf et al. (2009)'s conclusion that better quantification of fine-scale resources could alter model predictions. Reducing the scale at which key resources are modeled and including more fine-scale estimates in model parameterizations could address this issue.

Resource availability across landscapes, however, is often seasonally variable (Kremen 2005). Examining NDVI (Normalized Difference Vegetation Index), Leong (2014) found that urban, agricultural and natural areas provided pulses of floral resources at different times of year. Further, pollinator abundance tracked these changes in resource availability. In Yolo County, sunflower blooms during a lull in blooming of hedgerow plants (Table A1). In 2013, a drought year, hedgerows in this study provided virtually no floral resources during the study period. Thus, at this time, resource abundance within weedy field margins and hedgerows may have been similar to one another than during different seasons or years, although over higher average resource availability is recorded in hedgerows in the spring-summer season (Morandin and Kremen 2013). This dearth of floral resources during the study period may partially explain the lack of effect of floral enhancements on bee nesting rates observed in this study.

Communities of native bees also fluctuate inter-annually (Petanidou et al. 2008) and seasonally within a year, with distinct flight periods of spring and summer bees (e.g. Ginsberg, 1983; Williams et al., 2001). As a result, services may fluctuate within or across years. While pollination models can account for seasonal variation of floral resources and pollinator populations, these models sum floral resources across seasons to generate a weighted average for a given parcel. Accounting for different seasons so as to reflect bloom times for crops and natural habitats may give growers a more relevant picture of pollinator availability during times of peak need.

Conclusions

Our findings indicate that fine-scale mapping of pollination services will better reflect potential pollination trends within a single crop field while mapping at a landscape scale can capture general pollination trends across an agricultural region (e.g. Chaplin-Kramer et al. 2011, Lonsdorf et al. 2009). Both scales can help inform farmers about the pollination potential they can expect given their landscape context and the local resources provided on their farms. Despite our limited sampling effort, we show that direct assessments of pollinator nesting and foraging can lead to predictions of potentially uneven pollination services in mass-flowering crop fields. Additional field-testing of factors that impact nesting and foraging will likely yield further insights into pollination-service delivery. Until current models can be parameterized with field data from multiple crops across many regions and at different time scales, altering existing models to better assess nesting resources and scaling foraging to floral resource density may enhance predictions of pollination services across scales.

Acknowledgements

We thank two anonymous reviewers for their insightful comments on this manuscript. Ashley Ellis and our other field assistants made fieldwork possible. We appreciate the members of the Kremen lab for their ideas and editing. We thank the three anonymous sunflower seed companies and all the farmers who let us sample on their land. This project was funded by a Western Sustainable Agriculture Education Research Grant to H.S.S., a National Institute for Food and Agriculture Predoctoral Fellowship to H.S.S., a National Science Foundation Graduate Fellowship to H.S.S., a USDA Conservation Innovation Grant 69-3A75-12-253 to the Xerces Society/C.K., an Army Research Office grant W911NF-11-1-0361 to C.K, and by the U.S. Department of Agriculture (USDA-NIFA 2012-51181-20105 to Rufus Isaacs, Michigan State University).

Literature Cited

U.S. Department of Agriculture, N.R.C.S. 2013. Soil Survey Geographic (SSURGO) database for Yolo County, California. ArcGIS 10.2. URL http://websoilsurvey.nrcs.usda.gov

Baddeley, A. and R. Turner. 2005. spatstat: An R Package for Analyzing Spatial Point Patterns. URL http://www.jstatsoft.org/v12/i06/

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. URL http://CRAN.R-project.org/package=lme4

Benjamin, F. E., J. R. Reilly, and R. Winfree,. 2014. Pollinator body size mediates the scale at which land use drives crop pollination services. Journal of Applied Ecology 51: 440–449.

Brosi, B. J., P. R. Armsworth, and G. C. Daily. 2008. Optimal design of agricultural landscapes for pollination services. Conservation Letters 1: 27–36.

Cane, J. H. 1991. Soils of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth and climate. Journal of the Kansas Entomological Society: 406–413.

Chaplin-Kramer, R., K. Tuxen-Bettman, and C. Kremen. 2011. Value of wildland habitat for supplying pollination services to Californian agriculture. Rangelands 33: 33–41.

Cox, D. R. and V. Isham. 1980. Point Processes, vol. 12. CRC Press. Boca Raton, FL, USA.

Esther Julier, H. and T. H. Roulston. 2009. Wild bee abundance and pollination service in cultivated pumpkins: farm management, nesting behavior and landscape effects. Journal of Economic Entomology 102: 563–573.

Frankie, G. W. 1973. A simple field technique for marking bees with fluorescent powders. Annals of the Entomological Society of America 66: 690–691.

Garibaldi, L. A., I. Steffan-Dewenter, C. Kremen, J. M. Morales, R. Bommarco, S. A. Cunningham, L. G. Carvalheiro, L.G., N. P. Chacoff, J. H. Dudenhoeffer, S. S. Greenleaf, A. Holzschuh, R. Issacs, K. Krewenka, Y. Mandelik, M. M. Mayfield, L. A. Morandin, S. G. Potts, T. H. Ricketts, H. Szentgyörgyi, B. F. Viana, C. Westphal, R. Winfree, and A-M. Klein. 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecology Letters 14: 1062–1072.

Ginsberg, H. S. 1983. Foraging ecology of bees in an old field. Ecology: 165–175.

Greenleaf, S.S. and C. Kremen. 2006. Wild bees enhance honey bees pollination of hybrid sunflower. Proceedings of the National Academy of Sciences 103: 13890–13895.

Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. Oecologia 153: 589–596.

Hegland, S. J. and L. Boeke. 2006. Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. Ecological Entomology 31: 532–538.

Ives, A.R. 2015. For testing the significance of regression coefficients, go ahead and log-transform count data. Methods in Ecology and Evolution. Advance online publication.

Jonsson, M., R. Bommarco, B. Ekbom, H. G. Smith, J. Bengtsson, B. Caballero-Lopez, C. Winqvist, and O. Olsson. 2014. Ecological production functions for biological control services in agricultural landscapes. Methods in Ecology and Evolution 5: 243–252.

Keitt, T. H. 2009. Habitat conversion, extinction thresholds, and pollination services in agroecosystems. Ecological Applications 19:1561–1573.

Kim, J., N. Williams, and C. Kremen. 2006. Effects of cultivation and proximity to natural habitat on ground-nesting native bees in California sunflower fields. Journal of the Kansas Entomological Society 79: 309–320.

Knowler, D. and B. Bradshaw. 2007. Farmers' adoption of conservation agriculture: A review and synthesis of recent research. Food Policy 32: 25–48.

Kremen, C. 2005. Managing ecosystem services: what do we need to know about their ecology? Ecology Letters 8: 468–479.

Kremen, C., N. M. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, S. G. Potts, I. Steffan-Dewenter, D. P. Vazquez, R. Winfree, L. Adams, E. E. Crone, S. S. Greenleaf, T. H. Keitt, A-M. Klein, J. Regetz, and T. H. Ricketts. 2007. Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. Ecology Letters 10: 299–314.

Leong, M. 2014. Bees in a Changing World: How land surface phenology, bee community distributions, and pollinator-plant interactions are impacted by urbanization and agriculture. Ph.D. thesis, University of California, Berkeley.

Long, R., and J. Anderson. 2010. Establishing hedgerows on farms in California. UCANR Publications.

Long, R., A. Corbett, C. Lamb, C. Reberg-Horton, J. Chandler, and M. Stimmann. 1998. Beneficial insects move from flowering plants to nearby crops. California Agriculture 52: 23-26.

Lonsdorf, E., C. Kremen, T. Ricketts, R. Winfree, N. M. Williams, and S. Greenleaf. 2009. Modelling pollination services across agricultural landscapes. Annals of Botany 103: 1589–1600.

Morandin, L. and C. Kremen. 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. Ecological Applications 23: 829–839.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2013. vegan: Community Ecology Package. R package version 2.0-10. URL http://CRAN.R-project.org/package=vegan

Paciorek, C. 2007. Bayesian smoothing with Gaussian processes using Fourier basis functions in the spectralGP library. R package version 1.3.1.

Parker, F.D. 1981 How efficient are bees in pollinating sunflowers? Journal of the Kansas Entomological Society: 61–67.

Parker, F. D., V. J. Tepedino, and G. E. Bohart. 1981. Notes on the biology of a common sunflower bee, Melissodes (Eumelissodes) agilis Cresson. Journal of the New York Entomological Society: 43–52.

Petanidou, T., A. S. Kallimanis, J. Tzanopoulos, S. P. Sgardelis, and J. D. Pantis. 2008 Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. Ecology Letters 11: 564–575.

Pinheiro J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team 2015. nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3.1-120, <URL: http://CRAN.R-project.org/package=nlme>.

Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman. and P. Willmer. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? Ecology 84: 2628–2642.

Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, and P. Willmer. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecological Entomology 30: 78–85.

R Core Team. 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Rademaker, M., T. De Jong, and P. Klinkhamer. 1997. Pollen dynamics of bumble-bee visitation on Echium vulgare. Functional Ecology 11: 554–563.

Rands, S. A. and H. M. Whitney. 2011. Field margins, foraging distances and their impacts on nesting pollinator success. PloS One 6: e25971.

Ricketts, T. H. and E. Lonsdorf,. 2013. Mapping the margin: comparing marginal values of tropical forest remnants for pollination services. Ecological Applications 23: 1113–1123.

Roulston, T. H. and K. Goodell. 2011. The role of resources and risks in regulating wild bee populations. Annual Review of Entomology 56: 293–312.

Sardiñas, H. S. and C. Kremen. 2014. Evaluating nesting microhabitat for ground-nesting bees using emergence traps. Basic and Applied Ecology 15: 161–168.

Schulp, C., S. Lautenbach, and P. Verburg. 2014. Quantifying and mapping ecosystem services: Demand and supply of pollination in the European Union. Ecological Indicators 36: 131–141.

Stockhouse, R.E. 1976. A new method for studying pollen dispersal using micronized fluorescent dusts. American Midland Naturalist: 241–245.

Stonehouse, D.P. 1996. A targeted policy approach to inducing improved rates of conservation compliance in agriculture. Canadian Journal of Agricultural Economics/Revue canadienne d’agroeconomie 44: 105–119.

Ullmann, K. U. 2015. The Role of Connectivity and Disturbance in Dynamic Landscapes: Squash Bees (Peponapis pruinosa) in Yolo County, California (Doctoral dissertation). ProQuest Dissertations and Theses ID 15002

Vaughan, M. and M. Skinner. 2008. Using Farm Bill programs for pollinator conservation. USDANRCS National Plant Data Center, online: http://www. xerces.org/wp-content/uploads/2008/11/using farm bill programs xerces society. pdf.

Venables, W. N. and B. D. Ripley. 2002. Modern Applied Statistics with S. Springer, New York, 4th edn. ISBN 0-387-95457-0. URL http://www.stats.ox.ac.uk/pub/MASS4

Waddington, K. D. 1980. Flight patterns of foraging bees relative to density of artificial flowers and distribution of nectar. Oecologia 44: 199–204.

Williams, N. M., E. E. Crone, T. H. Roulston, R. L. Minckley, L. Packer, and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. Biological Conservation 143: 2280–2291.

Williams, N. M., R. L. Minckley, and F. A. Silveira. 2001. Variation in native bee faunas and its implications for detecting community changes. Conservation Ecology 5: 7.

Williams, N. M., J. Regetz, and C. Kremen. 2012. Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. Ecology 93: 1049–1058.

Williams, N. M. and R. Winfree. 2013. Local habitat characteristics but not landscape urbanization drive pollinator visitation and native plant pollination in forest remnants. Biological Conservation 160: 10–18.

Zurbuchen, A., S. Cheesman, J. Klaiber, A. Müler, S. Hein, and S. Dorn. 2010. Long foraging distances impose high costs on offspring production in solitary bees. Journal of Animal Ecology 79: 674–681.

Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer.

Tables

Table 1. Model results for incidence, abundance and richness of bees nesting in sunflower fields and edges. Values are effect sizes. Significance for the abundance model was determined using a parametric bootstrap on the likelihood ratios of models with and without the variable of interest

Covariate	Incidence	Abundance	Richness
Hedgerow presence	-4.855	-0.144	-0.081
Distance into field	-0.215†	-0.445**	-0.001†
Hedgerow presence x Distance	-0.005	-0.092†	-0.001
Soil particle size	0.038	0.210	0.006
Soil heterogeneity	1.317*	0.381†	0.183†
Percent bare ground	0.007	0.333†	0.001
Slope	0.051**	0.413**	0.009**
Soil hardness	-0.180	-0.092	-0.020

† P < 0.1, * P < 0.05, ** P < 0.01

Table 2. Effect of hedgerow presence, distance, and collection factors on the number of dye marks observed up to 50 m into sunflower fields.

Covariate	Estimate
Hedgerow presence	0.139
Distance into field	-0.155***
Hedgerow presence x Distance	0.014
No. bees marked	0.559*
Proportion female:male marked	0.066

* P < 0.05, *** P < 0.001

Appendix A: Site and soil characteristics for hedgerow and control sites in emergence trap nesting study

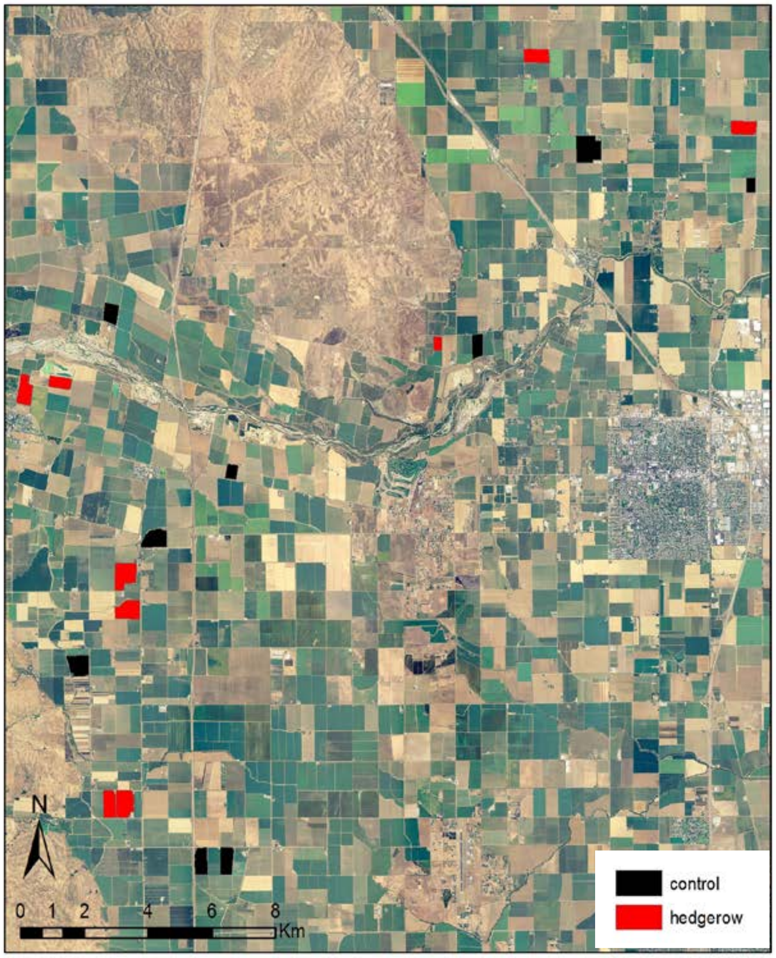


Figure A1. We sampled 18 sunflower fields, 9 control sites (black) next to weedy/bare field edges and 9 sites adjacent to hedgerows (red), in 2012 and 2013 in Yolo Co., California.

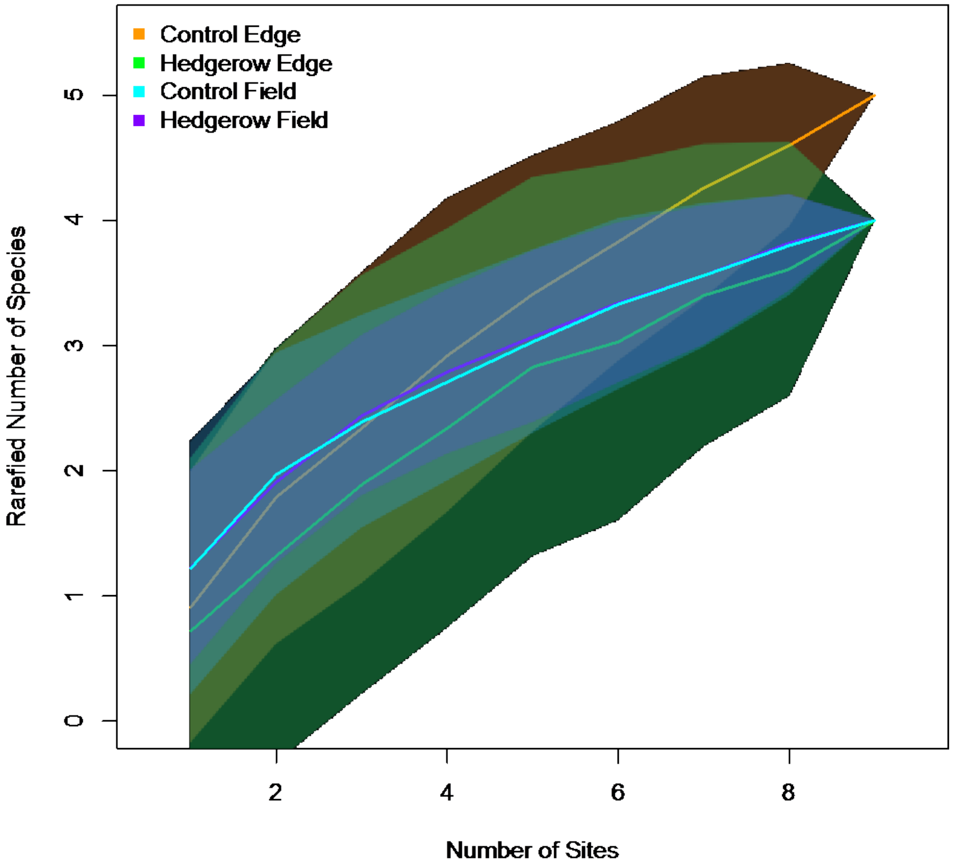


Figure A2. Rarefied number of species collected in emergence traps in hedgerow and control edges, and sunflower fields adjacent to hedgerows and controls.

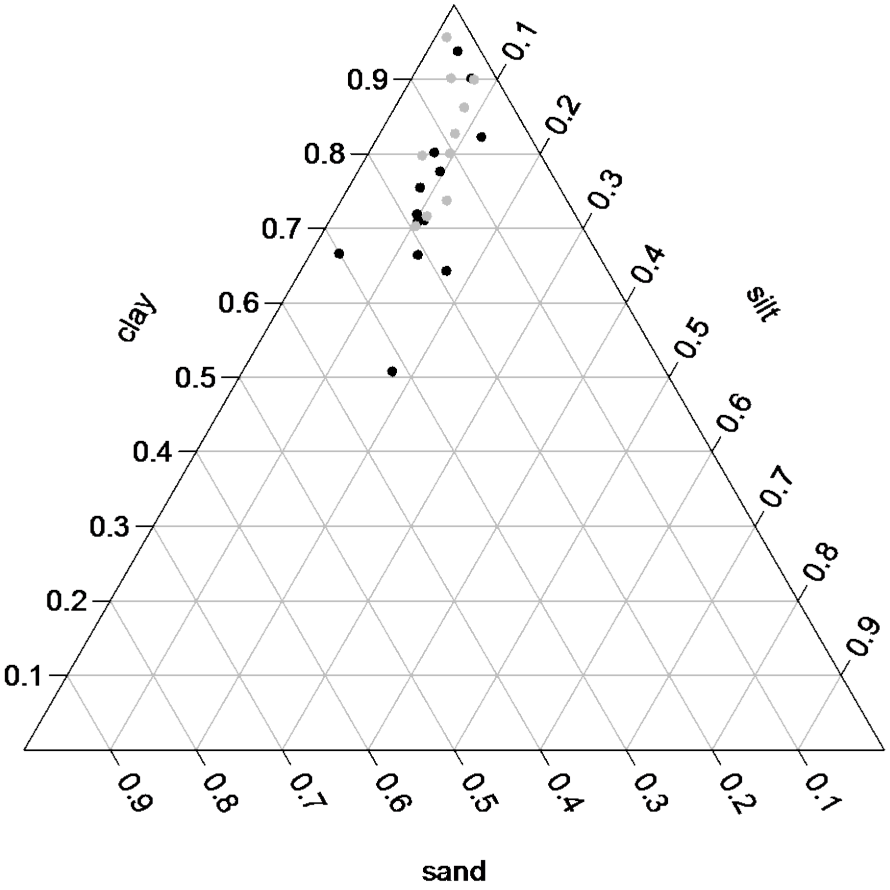


Figure A3. Percent sand, silt and clay in soil samples from hedgerows and (black circles) and controls (grey circles). All samples had extremely high clay content.

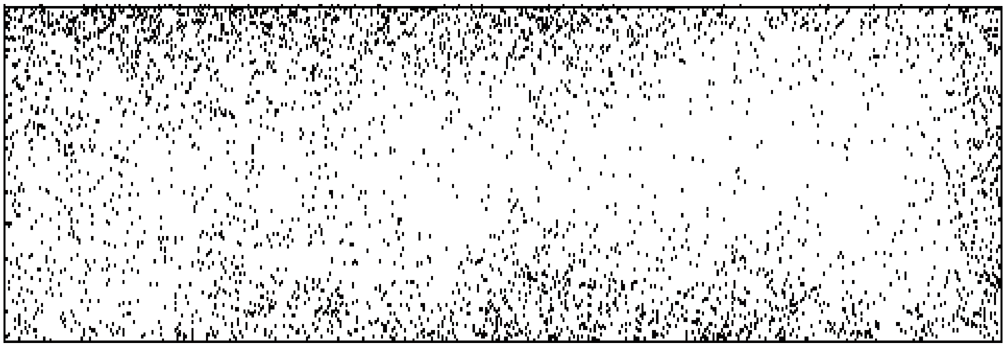


Figure A4. Density of nests drawn from a Poisson distribution, but with an edge effect for each pixel (an exponential of 5% times the distance for the density draw from the Poisson).

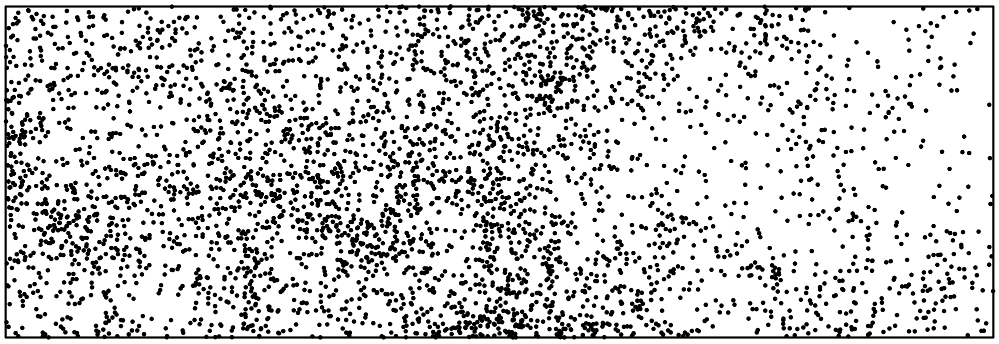


Figure A5. Density of nests drawn from a Poisson distribution, but without an edge effect.

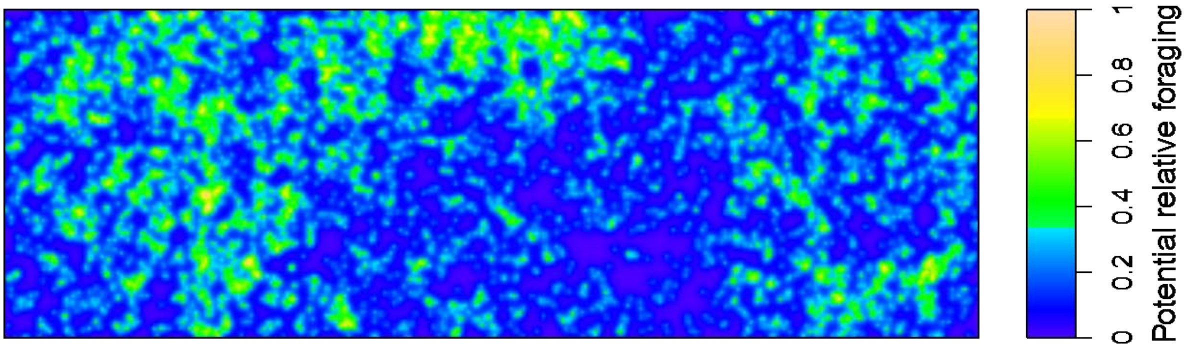


Figure A6. Predicted pollination coverage in a field where nesting was not clustered around field edges, but instead evenly distributed. We would still expect to see pollination centralized around nest location, which may exhibit other forms of spatial clustering within fields.

Table A1. Plant species in bloom in hedgerows and weedy edges during sunflower bloom. Numbers indicate the percent bloom summed from fifty 1 m^2 quadrats at each site.

Scientific Name	Common Name	Status	2012	2013
Achillea millefolium	Yarrow	hedgerow forb	1	0
Asclepias californica	milkweed	hedgerow forb	3	0
Asclepias fascicularis	milkweed	hedgerow forb	3	0
Aster chilensis	aster	hedgerow forb	1	0
Brassica sp.	mustard	weed	16	2
Centaurea solstitialis	yellow-star thistle	weed	1	1
Convolvulus arvensis	bindweed	weed	30	21
Daucus carota	wild carrot	weed	32	0
Eriogonum fasiciculatum var. fasiciculatum	buckwheat	hedgerow shrub	31	5
Foeniculum vulgare	fennel	weed	2	0
Grindelia	gumplant	hedgerow forb	3	0

camporum				
Heteromeles arbutifolia	toyon	hedgerow shrub	10	0
Latuca serriola	prickly lettuce	weed	0	0
Malvella leprosa	alkalai mallow	weed	0	0
Picris echioides	Bristly ox-tongue	weed	1	0
Polygonum arenastrum	knotweed	weed	7	0
Raphanus raphanistrum	wild radish	weed	0	0
Sambucus nigra ssp. cerullea	elderberry	hedgerow shrub	0	0
Solanum carolinense	Carolina horsenettle	weed	1	0

Table A2. Nest site indicators used to determine nesting habitat quality. Adapted from Sardiñas and Kremen 2014; Potts et al. 2005.

Nest variable	measurement
Bare ground	% bare exposed soil
Cavities	Number of holes > *or* < 2 cm
Cracks	% area covered with cracks
Litter	% leaf litter or duff
Wood	% dead dried wood
Rocks	% ground covered with rocks
Slope	Average of 3 different points within an e-trap using a slope finder
Soil compaction	Surface sol resistance (04.5 kgf cm^2) measured using a soil penetrometer Model no. 77114, Forestry Suppliers, Inc., Jackson, MA, USA
Vegetation	% area covered with live vegetation

Table A3. Species collected in emergence traps and specimens marked with luminous powder.

Species	Nesting habit	Sunflower specialization	Body size	e-trap field	e-trap edge	# marked females	# marked males
Anthophora urbana	solitary	generalist	medium	0	1	0	0
Diadasia enavata	solitary	specialist	medium	0	0	59	24
Halictus ligatus	social	generalist	small	0	1	NA	NA
Halictus tripartitus	social	generalist	small	0	1	NA	NA
Lasioglossum incompletum	social	generalist	tiny	30	35	NA	NA
Megachile parallela	solitary	specialist	medium	0	1	90*	21*
Melissodes agilis	solitary	specialist	medium	13	0	428	110
Melissodes lupina	solitary	specialist	medium	6	2	0*	0*
Peponapis pruinosa	solitary	specialist†	medium	0	0	4	0
Sphecodes	parasitic	generalist	tiny	3	0	NA	NA

sp. B							
Svastra obliqua expurgata	solitary	specialist	large	0	1	NA	NA
Triepeolus heterurus	parasitic	generalist	medium	0	1	6	1

* We did not differentiate between species within genera during powder marking

† *P. pruinosa* is a cucurbit specialist

Literature Cited

Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, and P. Willmer. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecological Entomology 30: 78–85.

Sardiñas, H. S. and C. Kremen. 2014. Evaluating nesting microhabitat for ground-nesting bees using emergence traps. Basic and Applied Ecology 15: 161–168.

Appendix B. Validation procedure for abundance model of ground-nesting bees collected in emergence traps

B.1 Validation Procedure for Abundance Model

We found that a negative binomial distribution better fit our abundance data (the standard deviation was not equal to the mean, a prerequisite for using the Poisson distribution with count data). Negative binomial models, however, are prone to high rates type I errors (Ives 2015). We therefore checked the type I error rate of our model. We randomized the values of each nesting characteristic, drawing from a uniform distribution with the same range as the characteristic we were evaluating. We then re-ran our model 100 times and calculated the proportion of times the nesting characteristic we randomized was significant. Through this process we discovered that our type I error rate was approximately 10% (twice as high as than the standard 5% type I error rate). We first attempted to log-transform our data, as suggested by Ives (2015), however the transformed data was not normally distributed (Shapiro-Wilk test, $W = 0.49$, $P < 0.001$). We then designed a parametric bootstrap (Booth 1995) that created a null distribution of the likelihood values from 1000 simulations of the model without the nesting characteristic of interest. We compared the p-values from the model that retained the variable of interest to this null distribution. We found that, in all cases, the p-values from our original model were confirmed by the parametric bootstrap. We report the test statistics from the bootstrap in Table 1.

Literature Cited

Booth, J. 1995. Bootstrap methods for generalized linear mixed models with applications to small area estimation. Statistical Modelling. Springer New York: 43-51.

Ives, A. R. 2015. For testing the significance of regression coefficients, go ahead and log-transform count data. Methods in Ecology and Evolution. Advance online publication.

Conclusion

Despite evidence indicating that hedgerows benefit communities of wild, native pollinators (Hannon and Sisk 2006; Morandin and Kremen 2013; M'Gonigle et al. 2015; Kremen and M'Gonigle 2015; Ponisio et al, *in press*), this study revealed that they are not a panacea for reversing recent declines in bee pollination services. Hedgerows neither increased yields of mass-flowering crops nor augmented nesting habitat above baseline conditions in agricultural field borders. These findings are not unsurprising given the tiny fraction of the landscape occupied by hedgerows compared to intensively managed cash crops.

The scale of hedgerow plantings may be mismatched to the scale of modern industrial farming. While increasing the number of hedgerows may partially address this problem, it may not go far enough. Proximity to large areas of natural habitat is the most important factor contributing to increased crop yields and buffering pollinator decline (Kremen et al 2004; Morandin and Winston 2005; Ricketts et al. 2008)

Agroecosystems are communities of plants and animals that have been shaped by human management, usually for production of food, fuel or fiber (Alteri 2002). Agroecological farming is modelled upon natural ecosystems, and thus encourages interactions between organisms and with their environment (Francis et al. 2008). As such, agroecological farming systems incorporate both natural and cropped diversity onto farm lands. Agroecological practices are emerging as capable of transforming harsh, homogenous agricultural landscapes into landscapes that more hospitable to biodiversity at multiple levels and thus supports a wide variety of ecosystem services. (Kremen and Miles 2012).

Hedgerows are but one diversification methods in a suite of agroecological techniques that include cover cropping, intercropping, and temporary insectary strips. Thus, hedgerows can be viewed as a tool in the diversification toolkit rather than a strategy to be employed in a stand-alone fashion. Hedgerows do not, for example, appear to improve nesting conditions for ground-nesting native bees (Chapter 3, though they may benefit nesting conditions for cavity-nesting bees (Kremen and M'Gonigle 2015). No-till cultivation may be a better management technique to focus on to improve conservation of on-farm populations of ground-nesting bees (Ullmann 2015). Multiple diversification techniques are likely complimentary (Kremen and Miles 2012), however additional research into the factors affecting bee biology, and nesting specifically, is necessary to develop comprehensive management strategies for improving wild pollinator habitat in agricultural landscapes.

Hedgerows are, nevertheless, an important conservation tool (Morandin and Kremen 2013; Kremen and M'Gonigle 2015; M'Gonigle et al. 2015; Ponisio et al., *in press*). Hedgerows support higher bee abundance (Morandin and Kremen 2013), increase the occurrence of rare species (M'Gonigle et al. 2015), enhance beta diversity (Ponisio et al., *in press*), and attract a functionally diverse community of pollinators (Kremen and M'Gonigle 2015). These conservation benefits, however, do not necessarily translate into increased levels of pollination services in these intensive landscape settings, particularly given the high pollination demands of monoculture mass-flowering crops. Thus, hedgerows alone will not solve the pollination crisis if used in the absence of other field- and landscape-scale diversification strategies that provide critical habitat and other pollen and nectar resources often lacking in intensive agricultural landscapes.

Literature Cited

Altieri, M.A. 2002. Agroecology: the science of natural resource management for poor farmers in marginal environments. *Agriculture, Ecosystems & Environment*, 93(1), 1-24.

Francis, C., G. Lieblein, S, Gliessman, T.A. Breland, N. Creamer, R. Harwood, L. Salmonsson, J. Helenium, D. Rickerl, R. Salvadow, M. Wiedenhoeft, S. Simmons, P. Allen, M. Alteri, C. Flora and R. Poincelot. 2003. Agroecology: the ecology of food systems. *Journal of sustainable agriculture*, 22(3): 99-118.

Hannon, L.E., and T.D. Sisk. 2009. Hedgerows in an agri-natural landscape: potential habitat value for native bees. *Biological conservation*, 142(10): 2140-2154.

Kremen, C., and A. Miles. 2012. Ecosystem services in biologically diversified versus conventional farming systems: benefits, externalities, and trade-offs. *Ecology and Society*, 17(4): 40.

M'Gonigle, L.K., L.C. Ponisio, K. Cutler, and C. Kremen. 2015. Habitat restoration promotes pollinator persistence and colonization in intensively managed agriculture. *Ecological Applications*, 25(6): 1557-1565.

Morandin, L A., and M.L. Winston. 2005. Wild bee abundance and seed production in conventional, organic, and genetically modified canola. *Ecological applications*, 15(3): 871-881.

Morandin, L.A. and C. Kremen. 2013. Hedgerow Restoration Promotes Pollinator Populations and Exports Native Bees to Adjacent Fields. *Ecological Applications*, 23(4): 829-839.

Ricketts, T.H., J. Regetz,I. Steffan-Dewenter, S.A Cunningham, C. Kremen, A. Bogdanski, B. Gemmill-Herren, S.S. Greenleaf, A.M. Klein, M.M. Mayfeild, L.A. Morandin, A. Ocheing, and B.F. Viana,. 2008. Landscape effects on crop pollination services: are there general patterns? *Ecology letters*, 11(5): 499-515.

Ullmann, K. 2015. The Role of Connectivity and Disturbance in Dynamic Landscapes: Squash Bees (*Peponapis pruinosa*) in Yolo County, California. Doctoral Dissertation, University of California, Davis, 85; 3706696