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Authors: Mallinger, Rachel E., Ternest, John J., Weaver, Sarah A.,
Weaver, James, and Pryer, Samantha

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Importance of insect pollinators for Florida agriculture: a systematic review of the literature

Rachel E. Mallinger^{1,*}, John J. Terner¹, Sarah A. Weaver¹, James Weaver¹, and Samantha Pryer¹

Abstract

Insect pollinators contribute significantly to global food production impacting both crop yields and quality, but the dependence of specific crops on insect pollinators can vary across production regions and cultivars. The state of Florida has a unique agroecosystem that supports temperate and tropical fruits, vegetables, and nuts, and these specialty crops likely have a high dependence on pollinators. We conducted a systematic review to quantify the role of insect pollinators for Florida agriculture, and to identify crops and cultivars for which recent research on pollination is lacking. For all crops, we determined the average yield losses incurred without insect pollination ("pollinator contribution value") by synthesizing previously reported values. We found that insect pollinators are required or beneficial for 47 different crops in Florida, or 43% of all plant crop species grown in the state. Major crops in the state with complete to high dependence on insect pollinators include blueberries, mangoes, melons, squashes, and tangelos; for these crops, insect pollinators contribute 75 to 100% of crop productivity. Other major crops in Florida that are moderately to highly dependent on pollinators include avocados, cucumbers, field tomatoes, grapefruits, green beans, oranges (select cultivars), peppers, southern peas, and strawberries, with pollinator contributions ranging from 30 to 74%. The contribution of insect pollinators exceeds \$50 million per crop per yr in Florida for 7 of its most valuable crops. Using production data at the county level, we found that pollinators contribute to agriculture in almost all Florida counties. Our review identified a number of crops for which little information on pollination requirements exists, especially for modern cultivars. We discuss gaps in our knowledge of crop pollination requirements and recommendations for future research. Estimates of pollinator contributions are invaluable for farm management and policy decisions around pollinator conservation.

Key Words: pollination; pollinator-dependency; fruit set; seed set; bees

Resumen

Los insectos polinizadores contribuyen significativamente a la producción mundial de alimentos afectando el rendimiento como la calidad de los cultivos, pero la dependencia de cultivos específicos de los insectos polinizadores puede variar entre las regiones de producción y los cultivares. El estado de Florida tiene un agroecosistema único favorable a la producción de frutas, verduras y nueces de zonas templadas y tropicales, y es probable que estos cultivos especiales tengan una alta dependencia de los polinizadores. Realizamos una revisión sistemática para cuantificar el papel que juegan los insectos polinizadores en la agricultura de Florida y para identificar cultivos y cultivares que le faltan investigaciones recientes sobre polinización. Para todos los cultivos, determinamos el promedio de las pérdidas de rendimiento incurridas sin la polinización de insectos ("valor de contribución de los polinizadores") sintetizando los valores reportados previamente. Descubrimos que los insectos polinizadores son necesarios o beneficiosos para 47 diferentes cultivos en la Florida, o el 43% de todas las especies de cultivos de plantas cultivadas en el estado. Los principales cultivos en el estado con una dependencia completa o alta de insectos polinizadores incluyen arándanos, mangos, melones, calabazas y tangelos; para estos cultivos, los insectos polinizadores contribuyen del 75 al 100% de la productividad de los cultivos. Otros cultivos importantes en la Florida que dependen de los polinizadores entre moderada y alta son los aguacates, pepinos, tomates, toronjas, frijól verde, naranjas (cultivares seleccionados), pimientos, guisantes sureños y fresas, con contribuciones de polinizadores que oscilan entre el 30 y el 74%. La contribución de los insectos polinizadores supera los \$50 millones por cultivo por año en Florida para 7 de sus cultivos más valiosos. Usando datos de producción a nivel de condado, encontramos que los polinizadores contribuyen a la agricultura en casi todos los condados de la Florida. Nuestra revisión identificó una serie de cultivos para los que existe poca información sobre los requisitos de polinización, especialmente para los cultivares mas modernos. Discutimos las brechas en el conocimiento sobre los requisitos de polinización de los cultivos y recomendaciones para futuras investigaciones. Las estimaciones de las contribuciones de los polinizadores son invaluable para el manejo de las granjas y las decisiones políticas relacionadas con la conservación de los polinizadores.

Palabras Clave: polinización; dependencia de polinizadores; set de frutas; conjunto de semillas; abejas

Insect pollinators are responsible for producing a significant portion of our food supply including many fruits, seeds, and nuts. While estimates vary, recent studies suggest that 35% of global agricultural production is animal (primarily insect) pollinated (Klein et al. 2007). The contribution of pollinators to human diets may be even more

significant given that animal-pollinated crops provide higher ratios of nutrients compared to wind-pollinated crops, such as grains, or crops that do not require pollination, such as tubers (Eilers et al. 2011). Demand for pollinator-dependent specialty crops is rising with increasing gross domestic product (GDP), thereby increasing the global

¹University of Florida, Department of Entomology & Nematology, Gainesville, Florida 32611-0620, USA; E-mail: rachel.mallinger@ufl.edu (R. E. M.), jterner@ufl.edu (J. J. T.), andersonsarah@ufl.edu (S. A.W.), weaverj@ufl.edu (J. W.), spryer@ufl.edu (S. P.)

*Corresponding author; E-mail: rachel.mallinger@ufl.edu

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demand for pollinators (Aizen & Harder 2009). Accurately estimating the need for pollinators for agricultural production is critical for informing agricultural management decisions such as renting pollinators, applying pesticides during crop bloom, or installing pollinator habitat, and can furthermore inform land-use and conservation policies aimed at conserving or enhancing insect pollinators. Here, we synthesize the known information on crop pollination requirements for all crops in Florida, a specialty crop state with a unique agricultural economy that produces a wide diversity of pollinator-reliant tropical and subtropical crops.

Crop pollination requirements can vary significantly; whereas some crops are entirely dependent on pollinators to set seed and fruit, other crops set fruit and seeds without the assistance of pollinators, but with total yields, crop quality, and crop nutritional value enhanced by animal pollination (Klein et al. 2007; Klatt et al. 2014; Wietzke et al. 2018; Nicholson & Ricketts 2019). Measuring crop pollination requirements can be challenging as, even within a crop species, pollination biology can vary across cultivars or varieties (Sarracino & Vorsa 1991; Ramírez & Davenport 2016; Mallinger & Prasfika 2017). Furthermore, the degree to which pollinators contribute to crop yields can vary across time and space with fluctuations in pollinator abundance, diversity, or visitation rates (Blanche et al. 2006; Isaacs & Kirk 2010; Bartomeus et al. 2014; Mallinger & Gratton 2015; Tamburini et al. 2019).

Crops highly dependent on pollinators typically have 1 or more of the following traits including temporal, biochemical, or morphological barriers to self-pollination, high pollen deposition requirements, and pollen not readily released or transferred by abiotic agents such as wind, agitation, and gravity. Even self-compatible crops can be highly dependent on insect pollinators; for example, many blueberry cultivars have partial to high degrees of self-compatibility, yet fruit set and yields are very low in the absence of insect pollinators due to low rates of pollen release and transfer without the aid of insects (Campbell et al. 2018; Martin et al. 2019). For these crops, pollinators can increase both the quality and quantity of pollen deposition to result in increased yields or crop quality (Aizen & Harder 2007).

Assessments of pollinator dependence and demand for pollinators are becoming more common as specialty crop production increases worldwide (Aizen et al. 2008, 2009; Barfield et al. 2015; Giannini et al. 2015). However, in-depth analyses of crop pollination needs still are lacking for many important production regions and crop commodities. Florida, USA, is uniquely situated in North America and produces a large diversity of both temperate and tropical crops. In this systematic review, we synthesize the literature on the pollination biology of all crops grown in Florida and provide estimates for the pollinator-dependency of each crop. To do this, we determined the pollinator contribution values for each crop as the average yield loss incurred in the absence of pollinators, averaged across previous studies. We thereby provide a detailed and updated assessment of known pollinator contributions to crop yields, and discuss research needs and knowledge gaps related to crop pollination for many of the world's leading crop commodities.

Systematic Review Search Criteria

Using the 2018 USDA National Agricultural Statistics Service (NASS) Census of Agriculture, we compiled a list of all plant crops grown in Florida including field crops, fruit, tree nuts, horticultural crops, and vegetables. We minimized redundancy by eliminating broad crop categories that also overlapped with individual crops (e.g., "grains"). We furthermore eliminated minor crops for which acreage was not listed. The final list included 110 unique plant crops grown in Florida (Table 1 in Supplement 1).

In order to determine which crops to investigate further for their dependence on insect pollinators, we used the following criteria: (1) The crop commodity is potentially the result of pollination including fruits, nuts, and seeds. All crop commodities that are unrelated to pollination and reproduction, including leaves, roots, shoots, and tubers, were assumed to have zero dependence on pollinators and were not further considered. (2) The crop plant is an angiosperm and excludes grasses (Poaceae). Grasses and gymnosperms were assumed to be primarily or entirely wind pollinated. (3) The crop is grown on 5 or more acres (> 2.02 ha) in Florida. (4) The crop is a single plant taxon and not a broad multi-taxa group for which pollination needs cannot be assessed (i.e., "greenhouse fruits and vegetables"). Using these criteria, our resulting list contained 56 crops (Table 1 in Supplement 1).

For all included crops ($n = 56$), we calculated the average contribution of pollinators to yields based on previously published studies. To assemble our list of sources, we used all papers cited in a past review of global crop pollination requirements (Klein et al. 2007) and additionally searched the literature using Google Scholar for additional papers published through 2019. For each crop, we searched the literature using the terms "crop name (common and scientific)" and "pollination" OR "crop name (common and scientific)" and "pollinator." We included studies in our calculations if they reported some measure of crop productivity (e.g., fruit/seed set, crop yield) as a function of either pollinator-exclusion treatments comparing pollinator-excluded with open-pollination treatments, or hand-pollination treatments comparing hand cross-pollinated with hand self-pollinated treatments (Supplement 2).

Of these 2 types of studies, pollinator-exclusion treatments arguably are a better assessment of pollinator contribution and typically are done through comparing fruit/seed set from flowers open to animal pollinators with that from flowers closed to animal pollinators using a fine mesh bag (Fig. 1). The limitation to this method is that it is dependent on the abundance, diversity, and efficacy of pollinators present, and thus only measures realized pollinator contributions and not maximum potential pollinator contributions. Hand-pollination treatments comparing fruit/seed set from flowers pollinated by hand with cross-pollen to those pollinated by hand with self-pollen (typically in a controlled environment) may be used instead to represent pollinator contributions because animal pollinators often facilitate cross-pollination even though self-pollination could occur in their absence. However, this comparison does not include the contribution of animal pollinators to self-pollination, thereby potentially underestimating animal pollinator contributions, or the contribution of wind to cross-pollination, thereby potentially overestimating animal pollinator contributions. Therefore, where possible, we used data from pollinator-exclusion treatments. We included only locally relevant data (Florida crop species/varieties or southeastern USA species/varieties) when available. When locally available data was not available, we averaged across all studies done in other regions.

Synthesizing Pollinator Contribution Values

For each study, we calculated the average pollinator contribution value as the proportion of the crop productivity attributed to pollinators. For studies that conducted pollinator exclusion experiments, this was calculated as (open pollination–pollinator excluded)/open pollination (Fig. 1), whereas for studies that compared hand pollination treatments, it was calculated as (cross–self)/cross. We estimated means for each treatment when they were presented graphically but not reported in the text. When differences between treatments were reported as statistically insignificant, we recorded the contribution value as zero.

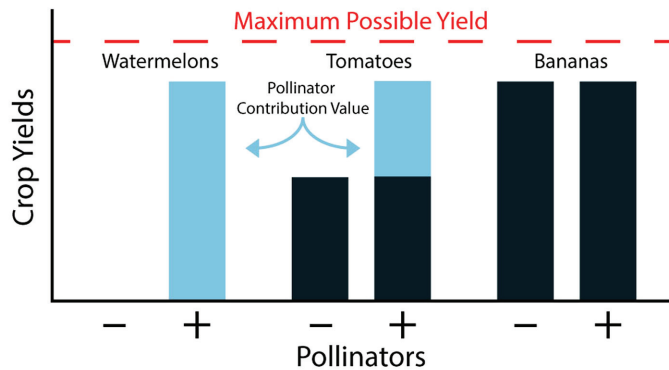


Fig. 1. Example pollinator contribution value for 3 hypothetical crops including banana (no value), tomatoes (moderate value), and watermelons (high value).

For studies measuring multiple crop response variables (e.g., fruit set, fruit weight, fruit quality), we used yield or total fruit/seed weight per plant or per area if reported. If not reported, we used percent fruit/seed set followed by individual fruit/seed weight. When response variables were measured over multiple studies, seasons, or crop varieties, we averaged values and report the range. Finally, in some cases, when pollination studies for a given crop were lacking, we used data from related congeneric crops.

Using acreage of each crop grown at the county level (USDA NASS 2018 Census of Agriculture County Data), we determined the relative pollinator dependency of agriculture in each Florida county. Dependence was calculated for each county as crop acreage per crop per county*average pollinator contribution value per crop (as a proportion, 0–1, Table 1), and summed across all crops. This value was then divided by the total area of the county to obtain relative pollinator dependency adjusted for area. Finally, we calculated the monetary value of insect pollinators as acreage*yield per acre*value per unit yield*average pollinator contribution value for 12 crops in Florida for which yield per acre, and value per unit of yield in Florida, were available from the 2018 USDA Census.

Role of Insect Pollinators in Florida Agriculture

Pollinators increase yields for 47 of the crops surveyed, which is roughly 43% of all plant-based crop commodities grown in Florida (Table 1). Of the crops surveyed, only 5 were found to not benefit from pollinators at all including bananas, figs (Florida fig species only), guavas, olives, and pineapples (Table 1). These crops are either parthenocarpic, producing seedless fruit without pollination and subsequent fertilization (e.g., bananas, figs [Florida species], and pineapple), or self-pollinate without the assistance of animal pollinators solely using gravity, agitation, or wind (e.g., olives). Pollinator contribution values could not be determined for 3 crops including Chinese peas, elderberries, and pecans, though the latter is known to be pollinated by wind (Wood 2000) (Table 1).

Pollinator contribution values were highest for watermelons, pumpkins, squash, passion fruit, cherimoya, and papaya, all of which are entirely dependent on pollinators to set fruit with pollinator contribution values of 100% (Table 1). However, the only research available on papaya pollination was conducted in East Africa where dioecious trees are grown (Martins & Johnson 2009), whereas in Florida the hermaphroditic cultivars available may be less dependent on insect pollinators (Crane et al. 1994). Crops with a high dependence on pollinators and high acreage in Florida (> 1,000 acres) include blueberries,

mangoes, cantaloupe, muskmelon, honeydew, tangerines, and tangelos; for these crops, pollinators contribute 75 to 99% of crop productivity (Table 1). For numerous high acreage crops including avocados, cucumbers, grapefruits, green beans, oranges, peppers, strawberries, southern peas, and tomatoes, pollinators contribute between 30 to 74% dependent on cultivar and context (Table 1). Crops with a low dependence on pollinators (10–20%) and high acreage in Florida include cotton, peaches, peanuts, and soybeans (Table 1). Finally, the range in pollinator contribution values for many crops was high, highlighting the variability in pollinator contributions across studies, crop varieties, and production systems (Table 1).

Crops for which insect pollinators have the highest monetary value include, in order: oranges, tomatoes, watermelons, grapefruits, blueberries, cucumbers, and peppers. For these crops, insect pollinators are estimated to contribute \$50 million or higher per crop per yr in Florida (Table 1).

South-central and southwest Florida have the highest dependence on insect pollinators for agricultural production, though pollinator-dependent agriculture is distributed throughout the state with insect pollinators contributing to agriculture in all but 2 counties (Fig. 2).

Limitations to Calculations of Pollinator Contribution Values

Pollinator contribution values can be highly sensitive to the crop productivity variables measured, as well as to the abundance, diversity, and efficacy of the pollinators present. Crop productivity variables differed across studies including initial fruit set, final fruit set, individual fruit/seed weight, and total fruit/seed weight (e.g., yield). Particularly for crops that are moderately dependent on pollinators, proportion fruit/seed set can underestimate pollinator value because flowers can set fruit or seed without animal pollination, but fruit/seed weights and subsequent yields will be lower (Rhodes 2002; Geslin et al. 2017). Alternatively, some plants compensate for poor pollination by allocating resources to produce heavier individual fruits and seeds, or to produce more flowers over time (Melathopoulos et al. 2014; Marini et al. 2015). In these cases, proportion fruit/seed set will be lower without animal pollination, but total yields will not be affected. Furthermore, pollination can affect the quality of the crop and its market value even when total yield is not increased with animal pollination (Langridge & Goodman 1985; Klatt et al. 2014; Wietzke et al. 2018), but crop quality generally was not measured across studies. Thus, pollinator contribution values can both overestimate and underestimate actual pollinator contributions, and are sensitive to the variables measured.

Additionally, pollinator contribution values will be determined by pollinator visitation rates and efficacy, which can vary considerably across contexts (Garibaldi et al. 2013; Kennedy et al. 2013). For crops with low pollinator contribution values, this may accurately reflect the crop's pollination requirements, or it may be due to a lack of pollinator activity. Thus, our values are a measurement of the realized pollinator value, which likely is lower than the potential pollinator value. Studies examining optimal yields with pollen supplementation may be the best measure of optimal pollinator contribution values, but this assumes that pollinators in theory can perform the function of supplemental hand pollination. Despite these limitations, our calculated pollinator contribution values are beneficial for showing the relative variation across crops and studies.

Another challenge in determining pollinator dependence is the lack of information on crop pollination biology for some crops. For many crops, the only available information is decades old and potentially irrelevant for modern cultivars. Specifically, we found a surprising lack of

Table 1. Average pollinator contribution values (APCVs) and their ranges for all crops included in this study. Average pollinator contribution values are compared to dependence values reported in Klein et al. (2007) including essential ($E \geq 90\%$ yield reduction without animal pollinators), great ($G, 40 - < 90\%$ yield reduction without animal pollinators), modest ($M, 10 - < 40\%$ yield reduction without animal pollinators), little ($L, > 0 - < 10\%$ yield reduction without animal pollinators), no increase (NI , no yield reduction without animal pollinators), increase-breeding (yields only increase with animal pollination during crop breeding but not in crop production), or not recorded (NR). The monetary value of insect pollinators (crop pollinator value) is calculated for 12 crops for which acreage, yield per acre, and value per unit yield in Florida were available from the 2018 USDA Census.

Crop	Scientific name	Acreage in FL	Value per acre in FL (\$)	Dependence (Klein et al. 2007)	Average pollinator contribution value (%)	Range in APCV (%)	Crop pollinator value (\$)	Sources (see Supplement 2 for full citations) along with response variable (FS = fruit/seed set, FW = individual fruit/seed weight, Y = yield, O = other, NA = not available)
Apples	<i>Malus domestica</i>	126	NA	G	66.6	19–93	NA	Mallinger & Gratton 2015 ^{FS} , Garratt et al. 2013 ^{FS} , Vizzotto et al. 2018 ^{FS} , Campbell et al. 2017 ^{FS} , Porcel et al. 2018 ^{FS}
Avocados	<i>Persea americana</i>	6,327	2,688	G	34	0–86	5,782,372	Davenport et al. 1994 ^{FS} , Perez-Balam et al. 2012 ^{FS}
Bananas	<i>Musa</i> spp.	312	NA	Increase-breeding	0	0	NA	Based on common knowledge that bananas are parthenocarpic
Blackberries	<i>Rubus</i> spp.	241	NA	G	39	27–51	NA	Pinzauti et al. 1997 ^{FS/NW} , Nybom et al. 1986 ^{FS}
Blueberries	<i>Vaccinium</i> spp.	7,147	11,692	G	83.5	74–93	69,774,875	Campbell et al. 2018 ^{FS} , Danko et al. 1993 ^{FS}
Cantaloupes, muskmelons	<i>Cucumis melo</i>	2,436	NA	E	99.4	97.5–100	NA	Eischen et al. 1994 ^{FS} , Bohn & Davis 1964 ^{FS} , McGregor & Todd 1952 ^{FS} , Revanasidda & Belavadi 2019 ^Y
Cherimoyas	<i>Annona squamosa</i>	31	NA	E	100	100	NA	Nagel et al. 1989 ^{FS}
Cherries	<i>Prunus avium</i> , <i>P. cerasus</i>	5	NA	G	97.5	95–100	NA	Holzschuh et al. 2012 ^{FS} , Freitas et al. 1999 ^{FS}
Chestnuts	<i>Castanea sativa</i>	323	NA	M	55.5	41–70	NA	Manino et al. 1991 ^Y , de Oliveira et al. 2001 ^{FS}
Chinese peas	<i>Pisum sativum</i> var. <i>saccharatum</i>	20	NA	NI	6.5	6.5	NA	Naeem et al. 2018 ^Y
Cotton	<i>Gossypium</i> spp.	98,569	NA	M	15.8	7.7–23.2	NA	Cusser et al. 2016 ^{NW} , Rhodes 2002 ^Y , Stein et al. 2017 ^{FS}
Cucumbers	<i>Cucumis sativus</i>	26,222	4,760	G	53.5	21–99	66,776,945	Dorjay et al. 2017 ^{FS} , Motzke et al. 2015 ^Y , Hossain et al. 2018 ^{FS/NW}
Eggplant	<i>Solanum melongena</i>	685	NA	M	49.6	13.5–91	NA	Gemmill-Herren & Ochieng 2008 ^{NW} , Amoaka & Yeboah-Gyan 1991 ^Y , Jlandong et al. 2004 ^Y , Amin et al. 2019 ^Y
Elderberries	<i>Sambucus nigra</i>	15	NA	M	NA	NA	NA	NA
Figs	<i>Ficus carica</i>	50	NA	M	0 ^a	0	NA	Anderson & Crocker 1994 ^{NA}
Grapefruit	<i>Citrus x paradisi</i>	40,248	2,453	L	73.5	67–80	72,565,333	Chacoff & Aizen 2007 ^{FS} , Wright 1937 ^{FS}
Grapes	<i>Vitis rotundifolia</i> , <i>V. spp.</i> hybrids	574	NA	NR	65 ^b	65	NA	Sampson et al. 2001 ^{FS}
Green peas	<i>Pisum sativum</i>	537	NA	NI	6.5	6.5	NA	Naeem et al. 2018 ^Y
Greenhouse tomatoes	<i>Lycopersicon esculentum</i>	14.69	NA	L	37.1	16.5–52.7 ^c	NA	Palma et al. 2008 ^{NW} , Banda & Paxton 1991 ^Y , Dogterom et al. 1998 ^{NW} , Yankit et al. 2018 ^Y
Guavas	<i>Psidium guajava</i>	678	NA	M	0 ^d	0	NA	Hedstrom 1988 ^{NA}
Honeydew	<i>Cucumis melo</i>	41	NA	E	99.4	97.5–100	NA	Eischen et al. 1994 ^Y , Bohn & Davis 1964 ^{FS} , McGregor & Todd 1952 ^{FS} , Revanasidda & Belavadi 2019 ^Y
Kumquats	<i>Citrus japonica</i>	59	NA	L	28 ^e	28 ^e	NA	NA
Lemons	<i>Citrus x limon</i>	272	NA	L	31	0–100	NA	McGregor 1976 ^{FS}
Lima beans	<i>Phaseolus lunatus</i>	625	NA	L	38.7 ^f	38.7 ^f	NA	NA
Limes	<i>Citrus latifolia</i> , <i>C. x aurantiifolia</i>	66	NA	L	22	0–44	NA	Sanford 1992 ^{FS} , McGregor 1976 ^{FS}
Loganberries	<i>Rubus x loganobaccus</i>	21	NA	NR	40	40	NA	Langridge & Goodman 1985 ^o
Macadamias	<i>Macadamia ternifolia</i>	109	NA	E	79.5	54–100	NA	Heard 1993 ^{FS} , Blanche et al. 2006a ^{FS} , Wallace et al. 1996 ^{FS} , Grass et al. 2018 ^{FS}

^aSpecific to fig varieties grown in Florida.

^bSpecific to muscadine and hybrid grape varieties grown in Florida.

^cYields from insect pollination compared to mechanical vibration for 3 of 4 studies on the crop.

^dData not shown: average pollinator contribution values based on description of data.

^eAverage pollinator contribution values based on averages across related crops including lemons, limes, and oranges.

^fAverage pollinator contribution values based on that for the related *Phaseolus vulgaris*.

^oData not shown: average pollinator contribution values based on description of data.

^YAverage pollinator contribution values specific to bell peppers, which make up the majority of pepper production in Florida.

Table 1. (Continued) Average pollinator contribution values (APCVs) and their ranges for all crops included in this study. Average pollinator contribution values are compared to dependence values reported in Klein et al. (2007) including essential (E, $\geq 90\%$ yield reduction without animal pollinators), great (G, $40 - < 90\%$ reduction without animal pollinators), modest (M, $10 - < 40\%$ reduction without animal pollinators), little (L, $> 0 - < 10\%$ reduction without animal pollinators), no increase (NI, no yield reduction without animal pollinators), increase-breeding (yields only increase with animal pollination during crop breeding but not in crop production), or not recorded (NR). The monetary value of insect pollinators (crop pollinator value) is calculated for 12 crops for which acreage, yield per acre, and value per unit yield in Florida were available from the 2018 USDA Census.

Crop	Scientific name	Acreage in FL	Value per acre in FL (\$)	Dependence (Klein et al. 2007)	Average pollinator contribution value (%)	Range in APCV (%)	Crop pollinator value (\$)	Sources (see Supplement 2 for full citations) along with response variable (FS = fruit/seed set, FW = individual fruit/seed weight, Y = yield, O = other, NA = not available)
Mangoes	<i>Mangifera indica</i>	2,672	NA	G	94	94	NA	Quenaudon et al. 2019 ^{FS}
Nectarines	<i>Persica laevis</i>	19	NA	G	39	39	NA	Nyeki et al. 1998 ^{FS}
Okra	<i>Abelmoschus esculentus</i>	343	NA	M	36	36	NA	Carr & Davidar 2015 ^{FS}
Olives	<i>Olea europaea</i>	65	NA	NI	0 ^h	0	NA	Giannini et al. 2015 ^{FS}
Oranges	<i>Citrus × sinensis</i>	422,421	1,947	L	31.1	26–36	255,783,097	Malerbo-Souza et al. 2004 ^{FS} ; Ribiero et al. 2017 ^{FS}
Papayas	<i>Carica papaya</i>	190	NA	L	100	100	NA	Martins & Johnson 2009 ^{FS} ; Martins 2007 ^{FS}
Passion fruit	<i>Passiflora edulis</i>	72	NA	E	100	100	NA	Junquiera & Augusto 2017 ^{FS}
Peaches	<i>Prunus persica</i>	1,025	NA	G	18	18	NA	da Mota & Nogueira-Couto 2002 ^{FS}
Peanuts	<i>Arachis hypogaea</i>	186,803	745	L	7.5	0–15	10,437,617	Blanche et al. 2006b ^{FS} ; Sanda et al. 2019 ^{FS}
Pears	<i>Pyrus communis</i>	85	NA	G	68.5	30–100	NA	Nyeki et al. 1993 ^{FS} ; Stephen 1958 ^{FS} ; Fountain et al. 2019 ^{FS}
Pecans	<i>Carya illinoensis</i>	8079	NA	NR	NA	NA	NA	NA
Peppers	<i>Capsicum</i> spp.	12,329	15,180	L	30.1 ^h	15.2–45	56,333,420	Pereira et al. 2015 ^Y ; Serrano & Guerra-Sanz 2006 ^Y
Persimmons	<i>Diospyros</i> spp.	266	NA	L	73	73	NA	Nikkeshi et al. 2019 ^{FS}
Pineapples	<i>Ananas comosus</i>	23	NA	Increase-breeding	0	0	NA	Gianini et al. 2015 ^{FS} ; Kudom & Kwapong 2010 ^{FS}
Plums, prunes	<i>Prunus domestica</i>	94	NA	G	65.2	61.8–68.6	NA	Langridge & Goodman 1985 ^{FS/FW}
Pomegranates	<i>Punica granatum</i>	146	NA	M	29.5	29.5	NA	Derin & Eti 2001 ^{FS}
Pumpkins	<i>Cucurbita maxima</i> , <i>C. pepo</i>	91	NA	E	100	100	NA	Artz & Nault 2011 ^{FS}
Raspberries	<i>Rubus</i> spp.	19	NA	G	45.3	29.3–69	NA	de Oliveira et al. 1991 ^{FS} ; Andrikopoulos & Cane 2018 ^{FS}
Sesame	<i>Sesamum indicum</i>	15	NA	M	43.3	31–55.5	NA	Stein et al. 2017 ^{FS} ; Das & Jha 2019 ^Y
Snap/green bean	<i>Phaseolus vulgaris</i>	27,823	NA	L	35.7	3–79	NA	Free 1966; Kingha et al. 2012 ^{FS} ; Ibarra-Perez 1999 ^Y ; Douka et al. 2018 ^{FS}
Southern peas	<i>Vigna unguiculata</i>	1,133	NA	L	34.7	18.5–63	NA	Fohouo et al. 2009 ^{FS} ; Auguste et al. 2019 ^{FS}
Soybeans	<i>Glycine max</i>	14,376	308	M	20.1	0–36	889,989	Milfont et al. 2013 ^Y ; Blettler et al. 2018 ^Y ; Kengni et al. 2015 ^Y ; Santos et al. 2013 ^Y ; Erickson et al. 1978 ^Y ; Chiari et al. 2005 ^Y
Squash	<i>Cucurbita</i> spp.	7,492	NA	E	100	100	NA	Klein et al. 2007 ^{FS}
Strawberries	<i>Fragaria</i> spp.	9,499	NA	M	38.4	27–56	NA	Klatt et al. 2014 ^{FW} ; Albano et al. 2009 ^Y ; Hodgkiss et al. 2018 ^Y ; Abrol et al. 2019 ^{FS} ; Castle et al. 2019 ^{FW}
Sunflower	<i>Helianthus annuus</i>	38	NA	M	22	0–42	NA	Mallinger et al. 2018 ^Y ; Tamburini et al. 2016, 2017 ^Y
Tangelos	<i>Citrus × tangelo</i>	1,975	3,513	NR	99.4	98.8–100	6,896,545	Mustard et al. 1965 ^{FS} ; Brown & Kresdorn 1969 ^{VA}
Tangerines	<i>Citrus tangerina</i>	9,499	2,154	L	83.5	67–100	17,084,806	Brown & Kresdorn 1969 ^{VA} ; Otero & Rivas 2017 ^Y
Tomatoes	<i>Lycopersicon esculentum</i>	29,136	13,916	L	50.6	33–73	212,053,789	Greenleaf & Kremen 2006 ^{FW} ; Bashir et al. 2018 ^{FW} ; Vinicius-Silva et al. 2017 ^{FW}
Watermelons	<i>Citrullus lanatus</i>	22,071	7,200	E	100	100	158,911,200	Kremen et al. 2002 ^{FS} ; Stanghellini et al. 1998 ^{FS} ; Free 1993 ^{FS}

^hSpecific to fig varieties grown in Florida.

^{VA}Specific to muscadine and hybrid grape varieties grown in Florida.

^YYields from insect pollination compared to mechanical vibration for 3 of 4 studies on the crop.

^{FW}Data not shown; average pollinator contribution values based on description of data.

^{FS}Average pollinator contribution values based on averages across related crops including lemons, limes, and oranges.

^{VA}Average pollinator contribution values based on that for the related *Phaseolus vulgaris*.

^{FW}Data not shown; average pollinator contribution values based on description of data.

^{FS}Average pollinator contribution values specific to bell peppers, which make up the majority of pepper production in Florida.

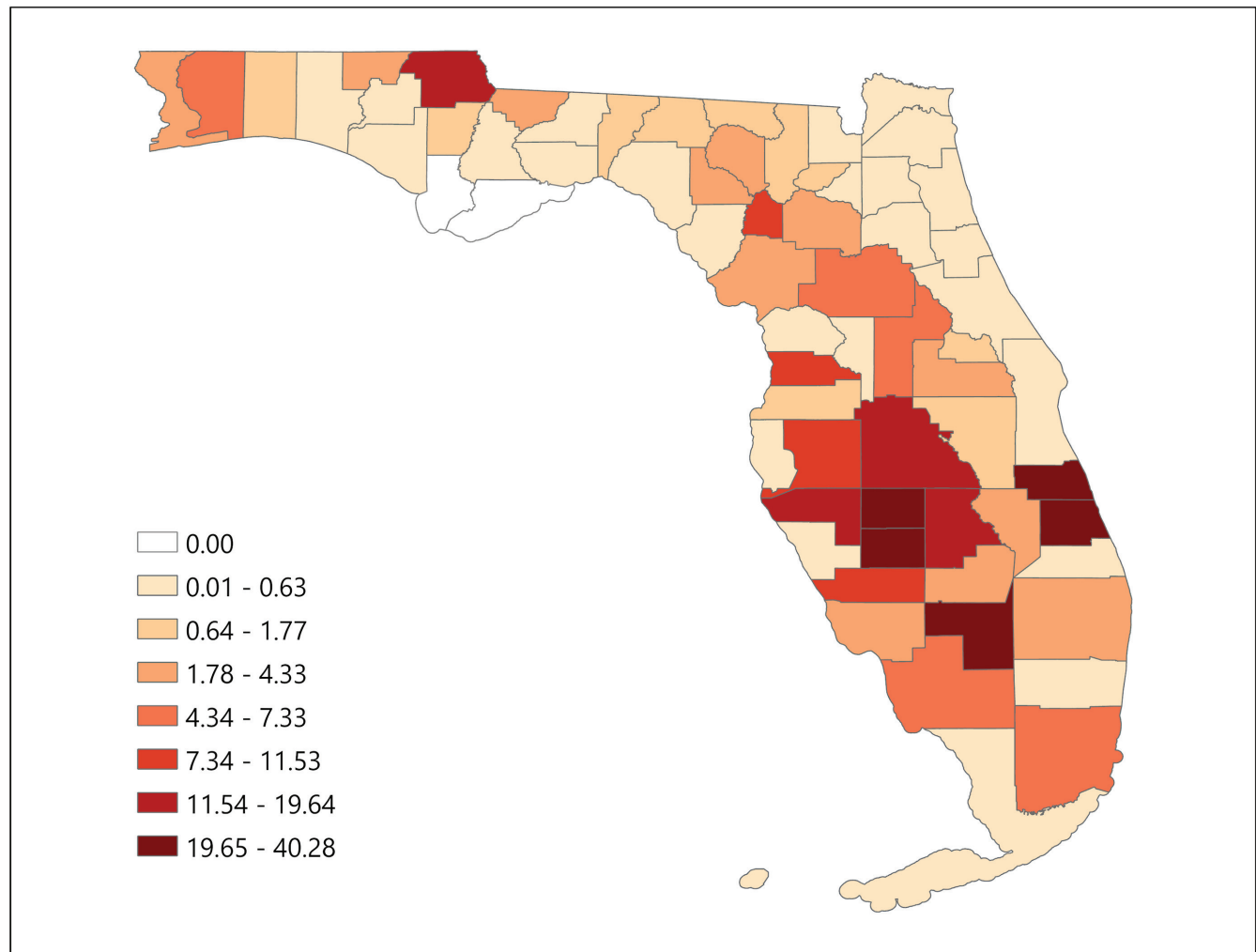


Fig. 2. Heat map showing the relative contribution of insect pollinators to agriculture in each county in Florida. Values were calculated as acreage per crop per county*average pollinator contribution value per crop (proportion 0–1), summed across all plant-based crops in each county and divided by the county's total area.

recent information for some melons (*Cucumis melo* L.; Cucurbitaceae), blackberries, tangelos, guavas, lemons, limes, nectarines, pears, and plums given the extent of their production worldwide. For other crops, the variability in pollinator contribution values was high, including crops such as cucumbers that generally are assumed to be dependent on pollinators. Some variability could be due to cultivar differences, while additional variability may be due to the difficulty of accurately estimating the contribution of wind pollination separate from animal pollination. Thus, we recommend that updated studies on the pollination ecology of these crops be conducted with modern cultivars.

Comparisons to Previously Reported Values

Variation in pollination requirements across cultivars explains some of the discrepancy between our findings and those previously reported in Klein et al. (2007). For example, figs are reported to be pollinator-dependent (Klein et al. 2007), but the cultivars grown in Florida are parthenocarpic and set fruit without pollination (Anderson & Crocker 1994). Alternatively, grapes are reported to receive no benefit from animal pollination (Klein et al. 2007), but studies done with the muscadine and hybrid grape varieties grown in Florida show that insect pollination improves yields (Sampson et al. 2001). Furthermore, pollination

requirements for citrus crops are highly variable as degrees of parthenocarpy, self-compatibility, and overall self-fertility vary across cultivars and species (Sanford 1992; Futch & Jackson 2003; Chao 2005). We found evidence for higher pollinator contributions to citrus crops than previously recorded (Klein et al. 2007), but this may reflect a publication bias in which cultivars thought to benefit from insect pollination are more frequently studied while cultivars with a known high degree of parthenocarpy are not studied. Such variation across cultivars can make it challenging to assess the need for pollinators at a local scale. However, at a larger scale, average pollinator contribution values can indicate relative pollinator dependence across crop commodities.

Contributions of Wild and Managed Pollinators

Both managed and wild pollinators contribute to crop pollination in Florida, though their contributions may not be equal. For example, in blueberries, crop pollination is provided almost exclusively by managed bees including honey bees *Apis mellifera* L. and bumble bees *Bombus* spp. (both Hymenoptera: Apidae) (Campbell et al. 2018), whereas a mixture of managed and wild bees pollinate watermelon (Campbell et al. 2019). Alternatively, non-bee pollinators such as flies may be important pollinators for mangoes, potentially exceeding man-

aged honey bees in their contributions (Sung et al. 2006; Huda et al. 2015). Of Florida's top 10 animal-pollinated crops, only 4 are consistently stocked with managed bees (blueberry, watermelon, cucumber, and squash) whereas the remaining crops receive pollination primarily from wild pollinators (strawberries, tomatoes, peppers, and green beans), or have highly variable densities of managed bees depending on the cultivar (oranges, grapefruits). Quantifying the relative contributions of different managed and wild pollinators would require additional information for each crop, including visitation rates and per-visit pollination efficacy of all pollinators. With this information, the value of key pollinators could be determined, thereby informing pollination management decisions and promoting the conservation or enhancement of important species.

Conclusions

In conclusion, we found that Florida's agriculture is highly dependent on insect pollinators due to the diversity of insect-pollinated crops, and this dependence is distributed across the state. Such high dependence on insect pollinators could increase variability in crop yields across both time and space (Garibaldi et al. 2011). Options to reduce variability and ensure good yields include (1) diversifying the use of managed pollinators, (2) enhancing the abundance or diversity of wild pollinators through on-farm plant diversification, off-farm habitat, and pollinator-friendly chemical use, and (3) optimizing pollinator efficacy through the timing and placement of managed pollinators or through pollinator attractants. Furthermore, reducing the need for pollinators through breeding crops for increased parthenocarpy or self-fertility may be an appealing option (Knapp et al. 2017). Future research should implement standard protocols to quantify crop pollination requirements across cultivars and farming contexts (Eckert et al. 2010).

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