

THE ROLE OF VARIETAL MIXTURES IN MEDIATING PEST CONTROL, YIELD, AND
ECONOMIC SERVICES IN AGROECOSYSTEMS

A Dissertation

Presented to the Faculty of the Graduate School

of Cornell University

in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

by

Lauren Denise Snyder

December 2019

© 2019 Lauren Denise Snyder

THE ROLE OF VARIETAL MIXTURES IN MEDIATING PEST CONTROL, YIELD, AND ECONOMIC SERVICES IN AGROECOSYSTEMS

Lauren Denise Snyder, Ph. D.

Cornell University

Agrobiodiversity can support ecosystem services that provide ecological, economic, and human nutritional benefits. Most efforts to capitalize on these services have focused on enhancing crop species diversity in the form of polycultures. While polycultures can provide numerous services, they can also present logistical challenges for farmers. One relatively under-explored form of diversification that may be more straightforward to implement is to enhance intraspecific crop diversity within a farm field by planting multiple varieties of the same crop species. Compared to different crop species, varieties of the same species are more likely to share agronomic traits that facilitate growing and marketing them together. While there is strong evidence that varietal mixtures can suppress pathogens and enhance crop yields, less is known about their ability to provide insect pest control services. Moreover, there is no empirical research on the performance of varietal mixtures across different landscape contexts, a factor known to influence the effectiveness of local-scale practices for pest control. Here, I investigate the potential for mixtures of *Brassica oleracea* varieties to provide profitable pest control services across different landscape contexts and elucidate the mechanisms underlying the effect of varietal mixtures on pest abundance and crop production. Chapter one provides an interdisciplinary synthesis of existing research on the capacity of varietal mixtures to provide pest control and yield services, strengthen agricultural resilience, and support human nutrition. In chapter two, I assess whether varietal mixtures of *B. oleracea* are a profitable pest management strategy on farms in New York State. I demonstrate the importance of accounting for landscape composition when implementing local-scale practices, as varietal mixtures can have both beneficial and detrimental effects on pest populations, depending on landscape context. This

chapter also indicates that enhancing trait variation in mixtures can increase profitability, potentially through reduced pest pressure. Chapter three explores the mechanisms underlying the effects of *B. oleracea* mixtures on pest populations and crop production, and suggests that varietal identity, rather than diversity per se, drives these processes. Collectively, my work demonstrates the importance of measuring multiple services to thoughtfully design varietal mixtures that contribute to sustainable food systems and support farmer livelihoods.

BIOGRAPHICAL SKETCH

Lauren grew up in the suburbs of Cleveland, Ohio. She discovered her passion for food systems as an undergraduate at Boston University (BU) where she had the opportunity to work as a field assistant on a project studying the agroecosystem services of bats in pecan orchards in Texas. During her undergraduate career, she also had the privilege of studying ecology abroad in Ecuador. It was here she found mentors who inspired her to apply her training as an ecologist and conservationist to tackle pressing environmental and social challenges. After graduating from BU with a B.A. in ecology and conservation biology, Lauren spent six months in Uda Walawe National Park in Sri Lanka researching solutions to human-elephant conflict in agricultural communities. After these experiences, she knew she wanted to pursue a PhD in ecology to conduct research that is both scientifically and socially important.

Dedicated to Scott and Steve who inspired this journey,
My parents, Anita, Ricardo, and Canela who loved and guided me along the way,
And Isa, Jamie, Kai, and Leo who are the future I fight for.

ACKNOWLEDGEMENTS

This dissertation is a product of the hard work and support of many. I thank my committee for guiding me and supporting my pursuit of interdisciplinary, applied research. I am grateful to my advisor, Dr. Alison Power, who enthusiastically gave me the space to explore my broad research interests. I would like to thank Dr. Jennifer Thaler for helping me tackle real-world problems using a strong scientific framework. I am grateful to Dr. Katja Poveda for her compassionate criticism and ability to streamline complex data into a cohesive story. I feel so fortunate to have worked closely with Dr. Miguel Gomez who welcomed me into the world of economics and was adventurous enough to embark on this interdisciplinary journey with me. I would also like to acknowledge Dr. Erika Mudrak, who I consider an honorary committee member. I will be forever grateful for her unwavering support, and the fearlessness and confidence with which she helped me tackle statistics. I am indebted to all the members of the Power lab who helped me plan and conduct my research, and who cheered me on along the way.

My dissertation research would not have been possible without the support of many farmers across the Finger Lakes Region of New York State. I am so grateful to all the growers who welcomed me onto their land and allowed me to explore their fields. Their enthusiasm and passion for producing food that nourishes people and the environment kept me going and continually reminded me why I set out on this path.

I could not have survived the challenges of graduate school without the support of my friends and family. I am so fortunate to be surrounded by strong, inspiring, and empathetic friends whose love and belief in me got me to the finish line. In particular, I am so thankful to have met Sharon Mier, whose compassion, wisdom, and humor kept me afloat. I am especially grateful to my California family, who loved, laughed, and danced with me through my last year of graduate school. Nothing I do would be possible without the support and love of my family; they have never stopped believing in and championing me. Finally, I am so lucky to have completed this journey with Ricardo and Canela by my side. I could not ask for more brave or loving companions.

TABLE OF CONTENTS

Biographical Sketch	iii
Dedication	iv
Acknowledgements	v
List of Figures	vii
List of Tables	viii
INTRODUCTION	1
CHAPTER ONE	7
<i>Crop varietal mixtures as a strategy to support ecological, economic, and nutritional services</i>	
CHAPTER TWO	40
<i>Landscape-dependent effects of varietal mixtures on insect pest control and implications for farmer profits</i>	
CHAPTER THREE	72
<i>Varietal identity, not varietal richness, predicts pest abundance and crop damage</i>	
APPENDIX	103
<i>Supplementary material</i>	

LIST OF FIGURES

Figure 1.1 Conceptual framework for comparing the services and economic implications associated with agricultural management practices.....	39
Figure 2.1 Relationship between flea beetle incidence and varietal richness across a gradient of landscape complexity.....	65
Figure 2.2 Effect of varietal richness on the incidence of <i>P. rapae</i> larvae across a gradient of landscape complexity.....	66
Figure 2.3 Effect of the number of varietal colors in a field on the abundance of <i>P. rapae</i> larvae across a gradient of landscape complexity.....	67
Figure 2.4 Relationship between crop damage and the abundance of <i>P. rapae</i> larvae.....	68
Figure 2.5 Relationship between crop damage and percent cropland in early season plantings of <i>B. oleracea</i> mixtures.....	69
Figure 2.6 Relationship between crop damage and percent cropland in late season plantings of <i>B. oleracea</i> mixtures.....	70
Figure 2.7 Effect of color richness on profitability.....	71
Figure 3.1 Effect of morphological composition on the abundance of <i>P. rapae</i> eggs and larvae, and <i>P. xylostella</i> larvae.....	95
Figure 3.2 Average number of pests in plots where kale is present or absent and where broccoli is present or absent.....	96
Figure 3.3 Effect of morphological composition on crop damage.....	97
Figure 3.4 Average crop damage when particular <i>B. oleracea</i> varieties are present or absent.....	98
Figure 3.5 Effect of color composition on the abundance of <i>P. xylostella</i> larvae.....	99
Figure 3.6 Average number of <i>P. xylostella</i> larvae when particular <i>B. oleracea</i> varieties are present or absent.....	100
Figure 3.7 Effect of color composition on crop damage.....	101
Figure 3.8 Average crop damage when particular <i>B. oleracea</i> varieties are present or absent...	102
Figure 2.S1 Relationship between percent cropland and the abundance of <i>P. rapae</i> larvae.....	110

LIST OF TABLES

Table 3.1 Description of crop damage scoring metric in morphology and color common garden experiments.....	94
Table 2.S1 List of agricultural inputs included in the crop budget analysis.....	103
Table 2.S2 Description of crop damage scoring in landscape analysis.....	104
Table 2.S3 Test of spatial autocorrelation of percent cropland at farm sites within three spatial scales in early and late season plantings of <i>B. oleracea</i> mixtures.....	105
Table 2.S4 Results of Mantel tests to evaluate spatial autocorrelation between farm fields and response variables in early and late season plantings of <i>B. oleracea</i> mixtures.....	106
Table 2.S5 Effect of varietal richness and color richness, percent cropland, and their two-way interactions on the incidence and abundance of flea beetles and <i>P. rapae</i> larvae.....	107
Table 2.S6 Effect of varietal richness and color richness on profitability, revenue, labor costs, and input costs.....	109
Table 3.S1 Results from linear mixed models testing for the effect of morphological richness on arthropod pest abundance, crop damage, and yield.....	111
Table 3.S2 Results from linear mixed models testing for the effect of morphological composition on arthropod pest abundance, crop damage, and yield.....	112
Table 3.S3 Results from linear mixed models testing for the effect of color richness on arthropod pest abundance, crop damage, and yield.....	113
Table 3.S4 Results from linear mixed models testing for the effect of color composition on arthropod pest abundance, crop damage, and yield.....	114

INTRODUCTION

A large body of research demonstrates a strong link between agrobiodiversity and the provisioning of numerous services, including pest suppression, crop productivity and yield stability (Andow 1991, Smithson and Lenné 1996, Power 2010, Letourneau et al. 2011, Iverson et al. 2014, Reiss and Drinkwater 2018), risk reduction and resiliency (Smithson and Lenné 1996, Lin 2011), and human dietary diversity (Frison et al. 2006, Toledo and Burlingame 2006). Polycultures are a common form of agrobiodiversity that can support many of these services (Poveda et al. 2008, Letourneau et al. 2011, Iverson et al. 2014). However, they may not be an ideal management strategy for all agricultural systems. In large-scale production systems, implementing polycultures can impede the use of mechanized equipment, resulting in higher labor costs (Gliessman 1985). Polycultures are also more knowledge intensive than simplified systems because farmers need to be versed in the growing requirements, production risks, and market opportunities associated with each crop species.

One alternative diversification strategy that may present fewer management constraints is to increase intraspecific crop diversity within a farm field by planting multiple varieties of the same crop species. Compared to different crop species, varieties of the same species are more likely to share agronomic characteristics that facilitate planting, harvesting, and marketing them together (Wolfe 1985, Wilhoit 1992). Varietal mixtures can also provide valuable ecosystem services; they have been shown to play an integral role in disease management programs (Zhu et al. 2000, Mundt 2002) and are increasingly recognized for their ability to enhance crop productivity (Reiss and Drinkwater 2018). However, fewer studies have evaluated the ability of varietal crop mixtures to support pest suppression services (Tooker and Frank 2012, Koricheva and Hayes 2018), and we know even less about the mechanisms that drive the effect of crop mixtures on arthropod communities in the field (Moreira et al. 2016). Despite growing recognition of landscape-level effects on local-scale management practices, little, if any, research has addressed the ability of varietal mixtures to support pest control services across different landscape contexts. Moreover, we lack empirical research on the impact of varietal mixtures on

production costs and farmer profits, which further constrains our ability to provide effective management recommendations to producers.

My doctoral research takes an interdisciplinary approach to addressing these knowledge gaps by 1) reviewing the potential for varietal mixtures to simultaneously support multiple services, 2) evaluating how varietal crop mixtures influence arthropod pests across different landscape contexts and whether they can enhance farmer profitability, and 3) exploring the mechanisms that underpin the effect of varietal mixtures on arthropod communities. To address the first question, I focused on varietal mixtures of annual crops grown for human consumption, and for questions two and three, I selected *Brassica oleracea* as my study system because this crop species encompasses a broad range of trait diversity (Ahuja et al. 2011), enabling me to easily test whether intraspecific variation in particular crop traits, such as plant morphology or color, mediate arthropod pest populations, crop damage, and crop yield. I evaluated the effect of varietal mixtures on three economically important cruciferous pests—the imported cabbageworm (*Pieris rapae*), the diamondback moth (*Plutella xylostella*), and flea beetles (*Phyllotreta* spp.)—to determine whether pests exhibited a universal response to intraspecific crop diversity or if responses varied across species.

In **Chapter one**, I evaluate an interdisciplinary body of literature to assess the potential for varietal mixtures to simultaneously support ecological, economic, and human nutrition services. Specifically, I explore the capacity of varietal mixtures to provide pest control and yield services, and discuss how these services can enhance an agricultural system's resilience to fluctuations in abiotic and biotic conditions. I also document intraspecific variation in nutrient content present in some crop species and consider whether this diversity can meaningfully expand dietary diversity to support human nutrition. Throughout the review, I systematically highlight areas in need of further research, information that is critical to making varietal mixtures a widely implemented diversification strategy. By linking typically disparate disciplinary approaches, I aim to advance our understanding of how to design multifunctional, resilient agroecosystems that improve food security and support livelihoods.

To understand the real-world impact of varietal mixtures on pest populations and farmer profits, I conducted a landscape-scale observational study on small-holder farms spread across the Finger Lakes Region of NY State. This work is described in **Chapter two**. I selected varietal mixtures that varied across two metrics of intraspecific crop diversity—varietal richness and number of plant colors (color richness). I evaluated the effect of varietal and color richness on crop damage, and the incidence and abundance of two pests, *P. rapae* and *Phyllotreta* spp. I assessed the context-dependency of these effects by sampling early and late season plantings of *B. oleracea* crops on farms spread across a gradient of landscape composition. To evaluate the economic impact of varietal mixtures, I created crop budgets for each plot to track input and labor costs, crop revenue, and farmer profits. I found context-dependent effects of varietal mixtures that varied across pest species. In early season plantings, increased varietal richness reduced *Phyllotreta* spp. incidence in simple landscapes, but the opposite trend emerged in complex landscapes. In contrast, the incidence and abundance of *P. rapae* larvae in late season plantings was negatively correlated with varietal and color richness, but only in complex landscapes. Using a net present value analysis, I found color richness was positively correlated with profits, likely due to increased revenue and a slight reduction in labor and input costs. These findings indicate that varietal mixtures can have significant impacts on pest populations, which are mediated at least partially by intraspecific variation in crop color. Moreover, this study demonstrated that varietal mixtures are a logistically feasible form of diversification that can enhance profitability. However, the effectiveness of varietal mixtures varied across landscape contexts and by pest species, suggesting mixtures must be designed and implemented thoughtfully to support pest suppression services.

In **Chapter three**, I home in on the mechanisms underpinning the relationships between varietal mixtures and pest abundance I observed in the landscape-scale observational study. Relatively little is known about the mechanisms driving the effects of varietal mixtures on pest abundance and crop production (Hughes et al. 2008, Moreira et al. 2016). However, hypotheses generated from species-level research on ecosystem processes provide a useful framework that

could be applied to research on varietal mixtures. This body of work suggests that biodiversity effects may be driven by multiple mechanisms related to either diversity per se (e.g., species richness) or the presence of a particular species. I apply this framework to varietal mixtures of *B. oleracea* to test two hypotheses: 1) varietal richness (e.g., diversity) drives the effect of mixtures on pest abundance and crop production, and 2) varietal identity drives the effect of mixtures on pest abundance and crop production. I leveraged the broad trait variation in *B. oleracea* varieties to test these hypotheses across two crop traits that are known to influence cruciferous herbivores, plant morphology and color. Specifically, I designed two common garden experiments to evaluate how mixtures of *B. oleracea* varieties that vary in morphology and color affect the abundance of two cruciferous pests (*P. rapae* and *P. xylostella*), crop damage, and yield. Across both insect pest species and both crop traits, I show that varietal identity, rather than varietal richness, mediates pest abundance and crop damage. These results suggest that pest management strategies that target influential varieties will be more effective than those focused on maximizing diversity per se.

Taken together, my dissertation research demonstrates that varietal mixtures are a viable on-farm diversification strategy that can simultaneously support ecological, economic, and nutritional services in certain contexts. However, accounting for landscape context and intentionally designing mixtures to incorporate certain varieties is critical for generating these services. While varietal mixtures are not a silver bullet solution for food security, they provide growers with another diversification option that can reduce logistical constraints associated with other forms of diversification. The research presented in the following chapters outlines remaining knowledge gaps and provides suggestions for future avenues of research that will enhance the implementation of varietal mixtures and further elucidate their capacity to support multiple services.

REFERENCES

- Ahuja, I., J. Rohloff, and A. M. Bones. 2011. Defence Mechanisms of Brassicaceae : Implications for Plant-Insect Interactions and Potential for Integrated. Pages 311–348 Sustainable Agriculture.
- Andow, D. a. 1991. Vegetational diversity and arthropod population response. *Rev. Entomol* 36:561–6.
- Frison, E., I. F. Smith, T. Johns, J. Cherfas, and P. B. Eyzaguirre. 2006. Agricultural Diversity , Nutrition , and Health : Making a Difference to Hunger and Nutrition in the Developing World. *Food & Nutrition Bulletin* 27:167–179.
- Gliessman, S. 1985. Multiple Cropping Systems: A Basis for Developing an Alternative Agriculture. Pages 69–86 Innovative Technologies for Lesser Developed Countries.
- Hughes, A. R., B. D. Inouye, M. T. J. Johnson, N. Underwood, and M. Vellend. 2008. Ecological consequences of genetic diversity. *Ecology letters* 11:609–23.
- Iverson, A. L., L. E. Marin, K. K. Ennis, D. J. Gonthier, B. T. Connor-Barrie, J. L. Remfert, B. J. Cardinale, and I. Perfecto. 2014. Do polycultures promote win-wins or trade-offs in agricultural ecosystem services ? A meta-analysis. *Journal of Applied Ecology* 51:1593–1602.
- Koricheva, J., and D. Hayes. 2018. The relative importance of plant intraspecific diversity in structuring arthropod communities: a meta-analysis. *Functional Ecology*:1–14.
- Letourneau, D. K., I. Armbrrecht, B. S. Rivera, J. M. Lerma, E. J. Carmona, M. C. Daza, S. Escobar, V. Galindo, C. Gutiérrez, S. D. López, J. L. Mejía, A. M. A. Rangel, J. H. Rangel, L. Rivera, C. A. Saavedra, A. M. Torres, and A. R. Trujillo. 2011. Does plant diversity benefit agroecosystems? A synthetic review. *Ecological applications* : a publication of the Ecological Society of America 21:9–21.
- Lin, B. B. 2011. Resilience in Agriculture through Crop Diversification: Adaptive Management for Environmental Change. *BioScience* 61:183–193.
- Moreira, X., L. Abdala-Roberts, S. Rasmann, B. Castagneyrol, and K. A. Mooney. 2016. Plant

- diversity effects on insect herbivores and their natural enemies: Current thinking, recent findings, and future directions. *Current Opinion in Insect Science* 14:1–7.
- Mundt, C. C. 2002. Use of multiline cultivars and cultivar mixtures for disease management. *Annual review of phytopathology* 40:381–410.
- Poveda, K., M. Gomez, and E. Martinez. 2008. Diversification practices: their effect on pest regulation and production. *Revista Colombiana de Entomologia* 34:131–144.
- Power, A. G. 2010. Ecosystem services and agriculture: tradeoffs and synergies. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 365:2959–2971.
- Reiss, E. R., and L. E. Drinkwater. 2018. Cultivar mixtures: A meta-analysis of the effect of intraspecific diversity on crop yield: A. *Ecological Applications* 28:62–77.
- Smithson, J. B., and J. M. Lenné. 1996. Varietal mixtures: a viable strategy for sustainable productivity in subsistence agriculture. *Annals of Applied Biology* 128:127–158.
- Toledo, Á., and B. Burlingame. 2006. Biodiversity and nutrition: A common path toward global food security and sustainable development. *Journal of Food Composition and Analysis* 19:477–483.
- Tooker, J. F., and S. D. Frank. 2012. Genotypically diverse cultivar mixtures for insect pest management and increased crop yields.
- Wilhoit, L. R. 1992. Evolution of herbivore virulence to plant resistance: influence of variety mixtures. Pages 91–119 *in* R. S. Fritz and E. L. Simms, editors. *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution and Genetics*. University of Chicago Press, Chicago.
- Wolfe, M. S. 1985. Prospects of Multiline Mixtures for Disease. *Annual review Phytopathol.* 23:251–273.
- Zhu, Y., H. Chen, J. Fan, Y. Wang, Y. Li, J. Chen, S. Yang, L. Hu, H. Leung, T. W. Mew, P. S. Teng, Z. Wang, and C. C. Mundt. 2000. Genetic diversity and disease control in rice. *Nature* 406:718–22.

CHAPTER ONE

CROP VARIETAL MIXTURES AS A STRATEGY TO SUPPORT ECOLOGICAL, ECONOMIC, AND NUTRITIONAL SERVICES

Lauren D. Snyder, Miguel I. Gómez, and Alison G. Power

Abstract

Most on-farm diversification strategies to enhance ecosystem services, such as pest control and yield, have focused on expanding crop species diversity. While polycultures often provide valuable services, logistical constraints with planting and harvesting can hamper implementation on large scales. One underexplored diversification alternative is to increase within-field intraspecific crop diversity through the use of crop varietal mixtures. In this review, we evaluate an interdisciplinary body of research to determine the potential for varietal mixtures of annual food crops to support food security by providing ecological, economic, and nutritional services. Previous literature synthesized the link between varietal mixtures and pest suppression and yield services. Here, we offer a new contribution by considering hypotheses generated from species-level research and assessing whether they also provide a useful framework for varietal mixtures. In addition, we evaluate the potential for varietal mixtures to increase farm resilience and growers' profits. While there is a growing effort to quantify the economic value of ecosystem services provided by agrobiodiversity in terms of enhanced yield or revenue, much less attention has been given to quantifying the production costs associated with diversification schemes. Consequently, we know little about the effect of diversification practices on farm profitability, the metric of ultimate importance to farmers. We address this issue by evaluating the ability of varietal mixtures to reduce production costs commonly associated with other types of agrobiodiversity and outline areas for future research to better understand the profit implications of varietal mixtures. Further, we review evidence that varieties of some crop species differ in phytochemical content—a functional trait important for pest suppression and human dietary diversity—suggesting that varietal mixtures could be designed to simultaneously support pest control and human nutrition services. Given that little research has explicitly addressed the

capacity for varietal mixtures to support human nutrition, we outline predictions for where we would expect to see the greatest nutritional impact of mixtures (e.g., primarily subsistence versus commercial agriculture systems), providing a foundation for future human nutrition research. Taken together, our review suggests that varietal mixtures are a promising and logistically feasible strategy that could simultaneously support multiple services.

1. Introduction

A large body of literature indicates agrobiodiversity can improve food security by sustaining a broad range of ecosystem services, such as arthropod pest suppression and crop productivity, which in turn provide economic and nutritional benefits to humans (Bianchi et al., 2006; Letourneau et al., 2011; Power, 2010; Tschardt et al., 2012; Fig. 1). While agrobiodiversity encompasses multiple levels of diversity, ranging from landscape diversity to intraspecific crop diversity (diversity within a crop species), most efforts to capitalize on the ecological, economic, and nutritional aspects of agricultural systems through diversification have focused on enhancing crop species diversity. For example, push-pull agroecosystems in Sub-Saharan Africa manipulate crop species diversity by intercropping maize, an important staple food crop, with desmodium (*Desmodium uncinatum*) and Napier grass (*Pennisetum purpureum*) to enhance arthropod pest control services and crop productivity, resulting in improved human nutrition and economic returns (Khan et al., 2008). While in many instances polycultures are a successful practice (Letourneau et al., 2011; Poveda et al., 2008), they can pose logistical challenges for growers (Fig. 1). For instance, polycultures are often not compatible with mechanized agricultural equipment, and they require more agronomic knowledge because crop species differ in their planting times, management and equipment needs, and marketability (Gliessman, 1985). Therefore, additional approaches to agricultural diversification could offer benefits to growers.

One relatively underexplored diversification strategy is to increase intraspecific crop diversity within a farm field by planting multiple varieties of the same crop species. Varietal

mixtures have been used quite extensively in disease control programs (Mundt, 2002), yet less consideration has been given to their ability to suppress arthropod pests (Tooker and Frank, 2012), and to provide the economic and nutritional benefits that can be associated with polycultures. Although much remains to be explored, a growing number of studies indicate that varietal mixtures can support arthropod pest suppression (Koricheva and Hayes, 2018; Tooker and Frank, 2012) and even more studies have demonstrated the beneficial impact of varietal mixtures on crop productivity and yield stability (Finckh et al., 2000; Reiss and Drinkwater, 2018; Smithson and Lenné, 1996). While, to the best of our knowledge, there have been no empirical economic analyses assessing the effect of varietal mixtures on farmer profits, we review several lines of evidence indicating varietal mixtures may improve agroecosystem resilience by helping buffer crop production from external shocks, and reducing some of the management complications and labor requirements associated with polycultures (Lin, 2011; Wilhoit, 1992). Furthermore, the potential for varietal mixtures to provide human nutritional services has yet to be rigorously explored. However, varieties of many crop species differ in their phytochemical content (Grusak and DellaPenna, 1999; Toledo and Burlingame, 2006), compounds important for plant defense as well as for human nutrition, which suggests that varietal mixtures could be designed to simultaneously support arthropod pest suppression and enhance human dietary diversity.

Here, we integrate perspectives from ecology, economics, and nutrition to evaluate the potential of varietal mixtures to serve as a practical, intermediate diversification strategy to simultaneously support several important ecosystem services in agroecosystems (Fig. 1). Although many ecosystem services contribute to food security, such as soil health, pollination (e.g. Gallai et al., 2009; Garibaldi et al., 2011; Klein et al., 2007), and disease control (e.g., Mundt, 2002; Power, 1991; Zhu et al., 2000), we limit the scope of this review to arthropod pest suppression and yield services. While we recognize the potential for varietal mixtures to improve ecosystem services in many cropping systems, such as perennial cropping systems or agroforestry, we focus this review on annual crops grown for human consumption, as these are

the systems in which most of the research on varietal mixtures has been conducted. We build on previous research exploring impacts of intraspecific crop diversity on yield and pest suppression (Koricheva and Hayes, 2018; Reiss and Drinkwater, 2018; Tooker and Frank, 2012), and expand to include economic and human nutrition dimensions of food systems. We map out areas for future research by highlighting knowledge gaps in our understanding of how varietal mixtures influence agroecosystem services that generate economic and nutritional benefits vital to food security.

2. Consequences of conventional agricultural intensification

Planting fields with one high-yielding crop variety has become the prevailing solution for providing food to a growing human population (Pingali, 2012). Yet, this practice has eroded valuable genetic resources that are foundational to creating resilient agroecosystems and has resulted in large areas of land dedicated to a relatively small number of crop species (Altieri, 1999; Karp et al., 2012). The lack of genetic diversity in monocultures often translates into enhanced vulnerability to abiotic and biotic stressors. Consequently, important ecosystem processes, such as nutrient cycling or pest regulation, are not self-sustaining (Altieri, 1999; Thrupp, 2000; Fig. 1). For instance, there are multiple examples from natural and agricultural systems demonstrating that reduced plant genetic diversity can aggravate pest problems over time (Belloti et al., 2012; Gallun, 1977; Peacock and Herrick, 2000; Pring and Lonsdale, 1989). To overcome these production challenges, conventional agriculture systems rely on repeated applications of external inputs, such as synthetic pesticides and fertilizers (Altieri, 1999). Although input-intensive agriculture can substantially increase yields in the short term, it also results in increased production costs and negative environmental externalities that are often under-valued (Tilman et al., 2002; Tschardt et al., 2012a). For instance, widespread reliance on pesticides in industrial practices has resulted in an unsustainable cycle of pesticide-resistance in insects and increased pesticide application, with environmental and human health consequences including water pollution, habitat degradation, reduction in natural enemy

populations, and chronic human health problems (Altieri, 1999; Dutcher, 2007; Geiger et al., 2010; Gibbs et al., 2009; Meehan et al., 2011; Tilman et al., 2002). For smallholder farmers in the developing world, reliance on synthetic fertilizers and pesticides is often impractical due to a lack of resources (Gurr et al., 2004). Therefore, exploring alternative agricultural management strategies that support multiple services is critical to creating self-sustaining, resilient food systems.

Moreover, the robustness of agricultural systems has historically been assessed based on crop yield, economic output, and cost-benefit ratios (McIntyre et al., 2009). However, it is increasingly recognized that these metrics fail to consider the diversity of nutrients provided by the agricultural system (DeFries et al., 2015), which is problematic as humans must consistently consume a wide range of nutrients (Graham et al., 2007). Today, a large percentage of the human population receives more than half of their calories and plant-based protein from just three crops—rice, wheat, and maize (Thrupp, 2000). Although yields have increased significantly (FAO, 2015), the associated reduction in crop diversity has resulted in human diet simplification, which is correlated with negative nutritional outcomes, such as micronutrient deficiencies, malnutrition, and obesity (Frison et al., 2006; Johns and Eyzaguirre, 2006; Fig. 1). Given the importance of micronutrients in supporting human health, it is vital that agriculture and nutrition interventions evaluate not only the yield capacity of agroecosystems, but their nutrient diversity as well (R. DeFries et al., 2015; Frison et al., 2006; Remans et al., 2011).

3. Evaluating the capacity of varietal mixtures to support ecosystem services

While much of the empirical and theoretical work on how biodiversity modulates agroecosystem functioning has targeted crop species diversity (Letourneau et al., 2011; Poveda et al., 2008), much less attention has been given to the role of varietal mixtures in agroecosystem processes, especially in terms of pest control (Tooker and Frank, 2012). Here, we use ecological theory on species mixtures as a framework to consider the potential yield and pest suppression benefits provided by varietal mixtures.

3.1. Varietal mixtures and productivity

Increased plant species diversity has been shown to enhance productivity through several mechanisms, including the selection effect, niche complementarity, and the microbial-mediated resources hypothesis (Hooper et al., 2005; Letourneau et al., 2011; Loreau and Hector, 2001; Reynolds et al., 2003). For instance, increasing the number of species in a plot translates into a higher probability of incorporating a very productive species (i.e., the sampling or selection effect) (Huston, 1997; Loreau and Hector, 2001). It is well established that cultivars vary in terms of productivity; therefore, the selection effect could be highly applicable to the relationship between varietal mixtures and productivity (Barot et al., 2017).

Polycultures are also expected to achieve high productivity through niche complementarity, where the species mixture is better able to exploit limited resources via resource partitioning or facilitation (Loreau, 2000; Loreau and Hector, 2001; Tilman et al., 1997). For example, different plant species may access nitrogen at different times during the growing season or from different regions of the soil, thereby reducing competitive interactions (Harrison et al., 2008). Although the variation in resource utilization among varieties of the same species would not be expected to be as pronounced as it is between species, cultivars of the same species can vary in their nutrient requirements or adaptations for accessing resources (Cowger and Weisz, 2008; Mundt, 2002; Ninkovic, 2003; Sarandon and Sarandon, 1995). For example, there is evidence that root depth and nutrient absorption efficiency differ among wheat cultivars (Lupton et al., 1974). A meta-analysis evaluating the effect of cultivar mixtures on crop yield identified facilitation as one possible mechanism underlying the increased yield stability observed in mixtures compared to monocultures (Reiss and Drinkwater, 2018). In addition, recent work has demonstrated that increased resource complementarity in plants can be selected for over time by growing plants in high diversity conditions, promoting niche differentiation that can enhance productivity (Zuppinge-Dingley et al., 2014). Thus, crop productivity in mixtures could be strengthened by incorporating varieties that have been intentionally selected in high diversity plantings (Zuppinge-Dingley et al., 2014). Moreover, the microbial-mediated

resources hypothesis proposes that species-specific soil microbes can further facilitate a plant's ability to differentially access limited resources (Reynolds et al., 2003). Research on microbial interactions across three cultivars of potatoes revealed cultivar-specific endophytic bacteria, soil microbes known to promote plant growth and health through beneficial metabolic interactions (Sessitsch et al., 2002). These findings suggest that niche complementarity and the microbial-mediated resources hypothesis could be relevant to varietal mixtures, at least in some systems.

However, several studies indicate that to achieve yield benefits mixtures must be designed thoughtfully; it is not varietal diversity per se that supports enhanced yields, but rather the functional components that are included in the mixtures and the ratio at which they are combined. For example, wheat mixtures have been shown to produce significantly higher grain protein content without sacrificing yield under low input conditions (Sarandon and Sarandon, 1995). However, this effect was dependent on nitrogen availability and the proportion of the mixture components. Other research has found grain yield and protein content in wheat mixtures to be highly correlated with the average of the cultivar components, which suggests mixture performance depends on the selection of cultivars (Gallandt et al., 2001). In addition, there is evidence that mixture efficiency is enhanced by mixture complexity; fields trials show that mixtures with three or more components tend to produce higher yields than mixtures with only two (Mille et al., 2006; Newton et al., 1997).

3.2. Varietal mixtures and arthropod pest suppression

In addition to enhancing crop productivity, there are a number of hypotheses derived from polyculture research predicting that increased plant diversity will support pest control services (Andow, 1991; Barbosa et al., 2009; Letourneau et al., 2011; Poveda et al., 2008; Root, 1973; Tahvanainen and Root, 1972; Thies et al., 2003). The resource concentration hypothesis posits that increased plant species diversity can directly suppress herbivore populations, particularly those that specialize on one plant species, by making it harder for herbivores to locate the appropriate host plant (Tahvanainen and Root, 1972). In contrast, monocultures

provide homogenous, concentrated resources that make it easier for specialist herbivores to locate a suitable host plant. For varietal mixtures to provide bottom-up control of herbivores they must be designed intentionally, using varieties that differ meaningfully in their defenses against herbivores. There are multiple examples of intraspecific variation in herbivore defenses that could be leveraged in the design of varietal mixtures, which we discuss in more detail below.

The natural enemies hypothesis suggests that increasing plant species diversity can also have negative, top-down effects on arthropod herbivores by increasing populations of natural enemies that benefit from an increase in different food sources, microhabitats, or chemical attractants (Haddad et al., 2009; Root, 1973). In addition, having “the right neighbor” can enhance both bottom-up and top-down control of herbivores, referred to as associational resistance (Barbosa et al., 2009; Tahvanainen and Root, 1972). The phenotypic diversity associated with increased intraspecific crop diversity in some crop species could enhance associational resistance by reducing herbivore detection of preferred varieties and by providing alternative resources or attractants for natural enemies. A recent study documented significantly lower aphid populations in barley mixtures compared to barley monocultures mediated by plant-plant volatile interactions (Dahlin et al., 2018). On the other hand, there is evidence that enhanced morphological diversity can inhibit top-down pest control by affecting the search pattern of natural enemies or by providing shelter to pests from predators (Peterson et al., 2016). Therefore, we may expect varietal mixtures characterized by high variation in morphological traits to receive less top-down pest control than mixtures with varieties that are relatively similar in structure.

Varietal mixtures have been used successfully in agricultural disease management programs for decades, often by including varieties that vary in their resistance to a pathogen. Varieties of the same crop species can also differ in their resistance to arthropod pests, which suggests a similar method could be used to provide pest control services. For instance, in response to herbivory by the Western corn rootworm (*Diabrotica virgifera*) most European lines of maize release a sesquiterpene, (E)- β -caryophyllene, which attracts an entomopathogenic

nematode that acts as a biological control agent of corn rootworm (Rasmann et al., 2005). However, most North American lines of maize are unable to induce this chemical distress signal in response to herbivory (Rasmann et al., 2005). Some plant-arthropod interactions even occur on a gene-for-gene basis, similar to many plant-pathogen systems. For instance, the Mi-1 gene in tomatoes has been found to confer resistance to some populations of *Macrosiphum euphorbiae* (potato aphid) and *Bemisia tabaci* (silverleaf whitefly) (Nombela et al., 2003; Rossi et al., 1998). Similarly, the Vat gene in melons provides increased resistance to *Aphis gossypii* (cotton aphid) and the transmission of viruses vectored by this aphid (Dogimont et al., 2009). The gene-for-gene interactions that occur between some arthropod species and crop varieties, as well as the diversity of plant defenses that can be found within a single crop species, indicate that varietal mixtures could be designed to modulate arthropod populations.

Previous work in natural and agricultural systems has demonstrated that increasing variation in plant traits and quality—at the individual, population, or community level—can either decrease or increase herbivore population size and may affect generalist and specialist pests differently (Andow, 1991; Underwood, 2004). Many crop species exhibit intraspecific variation in traits related to pest resistance, which suggests that crop varietal mixtures would likely affect pest populations. Indeed, a recent meta-analysis demonstrated that, on average, herbivore abundance is significantly reduced in varietal mixtures compared to monocultures (Koricheva and Hayes, 2018). We refer readers to Tooker and Frank (2012) for an exhaustive review of the literature on the pest control potential of varietal mixtures.

In spite of the potential for varietal mixtures to support pest control services, additional empirical research is needed to better understand when we should expect varietal mixtures to suppress or enhance pest populations as well as how these effects will influence herbivory. We also need more research across cropping systems, as varietal mixtures of certain crop species may be more effective than others depending on the level of intraspecific trait variation present. Moreover, crops are often attacked by a complex of pest species; therefore, we need research across arthropod taxa as well as studies that consider the effect of mixtures on multiple pest

species simultaneously. Studies testing the effects of varietal mixtures on different trophic levels would provide valuable information on whether the suppressive effects of mixtures are a function of bottom-up or top-down control of arthropod pests (Tooker and Frank, 2012). There is strong evidence that the success of on-farm management practices is often affected by the composition of the surrounding landscape (Tschardt et al., 2012b). Therefore, we need landscape-scale studies that examine the ability of varietal mixtures to support pest control services across different landscape contexts.

4. The potential for intraspecific crop diversity to support resilient agroecosystems

Agricultural producers are already experiencing negative effects of global climate change, making it increasingly important to design resilient agricultural systems that can withstand greater climate variability while continuing to promote agricultural and food system health (Döring et al., 2015; Lin et al., 2008). We use the term resilience to refer to an agroecosystem that continues to supply services, such as food production and pest control, when challenged with abiotic and biotic stressors. Biodiversity supports ecosystem function by enhancing complementary resource use and functional redundancy, which are important in the face of environmental change. The concept of functional redundancy is linked to the insurance hypothesis (Yachi and Loreau, 1999), the idea that biodiversity acts as a buffer against environmental variability because species differ in their response to change, helping to ensure the maintenance of an agroecosystem's functional capacity even in the face of external shocks.

Research has demonstrated that biodiversity, across time and spatial scales, can promote economically valuable ecosystem services that enhance agroecosystem functioning and stability. For example, preserving forest habitats at the landscape-scale can enhance pollination services resulting in higher coffee yields, an ecosystem service with an estimated value of \$60,000 annually for a single large farm (Ricketts et al., 2004). Similarly, polycultures can reduce insect pest and disease pressure, and enhance yields (Iverson et al., 2014; Letourneau et al., 2011; Power, 2010), and establishing diversified crop rotations can increase crop yield stability and

resilience to environmental stressors (Gaudin et al., 2015). The value of such services is typically determined by quantifying yield differences between diversified and simplified systems.

However, production output is only part of the story; costs associated with production (e.g., labor and inputs) must also be taken into account if we wish to assess the capacity of these diversification strategies to provide farmers with secure livelihoods. For instance, manipulating landscape-level diversity would require coordinated efforts among multiple stakeholders, which can be difficult to achieve (but see Brier et al., 2008; Murray et al., 2005; Schellhorn et al., 2015), and would likely entail higher costs that could dampen profits. Polycultures are often incompatible with mechanized agricultural equipment, and can increase cost due to higher labor requirements (Gliessman, 1985; Tooker and Frank, 2012).

Developing alternative diversification strategies that mitigate these costs would increase the options available to growers, allowing them to implement a form of diversification that meets their particular needs. Crop varietal mixtures are one alternative form of diversification that could promote resilient agroecosystems by providing valuable ecosystem services while also reducing logistical constraints associated with other scales of diversification. Unlike landscape-scale diversification, which growers have little control over, varietal mixtures can be easily implemented at the field scale. Varieties of a single species are more likely to have similar harvest schedules compared to crops of different species (Wolfe, 1985), and are often similar enough to be planted, harvested, and marketed together (Wilhoit, 1992). Although development times can vary across varieties, if mixtures are designed to incorporate varieties with similar agronomic characteristics, this problem can be avoided. Alternatively, many small-scale, tropical farmers intentionally plant fields to varieties that vary in maturation time to extend the growing or harvest period, spread out labor demands over a longer time period, and increase harvest security (Clawson, 1985). Management practices for different varieties of the same species are also likely to overlap, which means farmers can maximize their existing agronomic knowledge by expanding varietal diversity in a crop they already grow. Therefore, implementing varietal

mixtures may not require significant changes to existing management practices or farmer knowledge (Tooker and Frank, 2012), or investment in new infrastructure.

While varietal mixtures are not a panacea for food security, they are a powerful strategy that could complement other forms of diversification. Varietal mixtures could be particularly useful in situations where growers face labor constraints and have little control over their surrounding landscape—making it difficult to manipulate landscape or crop species diversity. Small-scale farmers in developing countries face poorly functioning markets and are often resource limited (Chavas and Di Falco, 2012); a management strategy that averts risk by increasing harvest security without incurring additional labor costs would be extremely valuable. By planting multiple varieties in a mixture, farmers mitigate risk by increasing the odds that at least some varieties will produce well, resulting in an overall harvest that might be adequate to sustain a livelihood. For example, in the highlands of Mexico, farmers routinely plant multiple varieties of potatoes together to reduce the spread of fungal pathogens (Ugent, 1968).

Planting varietal mixtures can also increase yield stability, particularly under conditions of environmental stress, which has important implications for growers who benefit from risk reduction and the ability to predict their annual production (Bullock et al., 2017; Kaut et al., 2009; Mundt, 2002; Smithson and Lenné, 1996). For example, under drought and low fertility conditions in Senegal, mixtures of early and intermediate maturity cowpea varieties produce more stable yields in comparison to monocultures (Thiaw et al., 1993). Early maturing varieties of cowpea are important to food security as they can provide food and income during times when food is scarce (Hall and Patel, 1985; Thiaw et al., 1993). However, medium maturity varieties tend to produce more grain and forage than the early maturity varieties (Thiaw et al., 1993). Planting a mixture of both varieties prolongs the period of food availability without sacrificing productivity. In Canada, wheat mixtures outperform wheat monocultures under nutrient-poor conditions and generate higher yields (Kaut et al., 2009). There have been similar findings with oats, where plots planted to multiple oat varieties were more productive than monocultures under drought stress (Peltonen-Sainio and Karjalainen, 1991). The ability of varietal mixtures to

outperform monocultures in the face of abiotic stresses indicates varietal mixtures have the potential to enhance the resilience of agroecosystems to climate change (Tooker and Frank, 2012).

However, due to a focus on measuring the value of services and a lack of data on costs, it remains unclear under what conditions varietal mixtures are likely to be a profitable diversification option. Future studies examining the economic impact of varietal mixtures should adopt a holistic approach that quantifies the costs of production as well as the value of ecosystem services generated by this scale of diversity. Such studies should be conducted over multiple years to assess the capacity of varietal mixtures to support sustainable livelihoods.

5. Varietal mixtures as a nutrition intervention

Given that over a quarter of the human population does not receive adequate nutrition, it is critical that nutritional benefits contributing to food security be recognized as an additional goal of agroecosystems (DeFries et al., 2015). However, the trend towards more simplified food systems has had negative impacts on human health and nutrition, such as low diet diversity, micronutrient deficiencies, and malnutrition in the developed as well as developing world (Frison et al., 2006; Graham et al., 2007; Negin et al., 2009). Despite global increases in agricultural productivity, more than 900 million people are still undernourished (FAO, 2010) and over 2 billion people exhibit at least one micronutrient deficiency (IFPRI, 2014). To address these issues, we cannot focus our attention solely on ramping up agricultural production, as this alone will not guarantee food security or improved nutrition (Herforth et al., 2012). Rather, we must pay attention to the diversity of food produced to increase food security and combat diet-related health issues (Esquinas-Alcazar, 2005; Herforth et al., 2012; Toledo and Burlingame, 2006). While we acknowledge that dietary diversity is likely most easily achieved by consuming different crop species, we highlight the meaningful nutritional diversity that exists within many annual food crop species.

Varietal mixtures may play an important role in diet diversification and human health as different crop cultivars vary in their nutrient compositions (Toledo and Burlingame, 2006). Moreover, many plant phytochemicals that are important to human nutrition also serve as plant defense compounds against insect herbivory. Recent research suggests that increasing nutrient heterogeneity within agroecosystems via intraspecific crop diversity could enhance pest control services (Wetzel et al., 2016). Therefore, increasing phytochemical diversity via varietal mixtures provides the opportunity to simultaneously enhance nutritional and ecological benefits. For example, carotenoids are not only important antioxidants for humans, they are also secondary metabolites key to plant defense (Hahlbrock and Scheel, 1989). Ascorbic acid, a vitamin critical to human nutrition, contributes to defending plants against photo-oxidative stress (Smirnoff, 1996). Significant variation in both compounds has been found among tomato varieties (George et al., 2004), suggesting that consuming a variety of cultivars could provide a more complete nutritional profile. Varieties of *Brassica oleracea* are also known to vary widely in their mineral nutrient composition and glucosinolate profiles—phytochemicals that offer protection from arthropod herbivores (Broadley et al., 2007). In the human gut, glucosinolates are hydrolyzed into isothiocyanates (Johnson, 2002) and there is strong evidence that these compounds play a major role in protecting against cancer (Talalay and Fahey, 2001). Indeed, research suggests that the variation in mineral composition found within *B. oleracea* crops is substantial enough to warrant use in genetic biofortification programs aimed at alleviating human dietary deficiencies, as varieties of this crop species can vary more than 20-fold in their concentrations of zinc (Broadley et al., 2007).

Varieties of staple crops, such as wheat can also differ significantly in their concentrations of magnesium and zinc (Oury et al., 2006). In some instances, the highest concentrations of these nutrients are found in rare, underutilized varieties. Zinc, which can only be acquired through diet, is an essential trace element that is vital to a range of human functions due to its role as a cofactor of many enzymes (Prasad, 1998). However, there is evidence that high magnesium and zinc content in grains comes at a cost to yield (Oury et al., 2006).

Therefore, it would be antagonistic to breed simultaneously for high nutrient content and yield (Oury et al., 2006) and to plant a field to just one cultivar would result in a tradeoff either in terms of yield or nutritional content. However, planting a mixture of wheat that includes both high yielding and nutrient-rich cultivars would allow yield and nutrition metrics to be met simultaneously.

Potatoes are another example of a staple food crop that encompasses broad variation in nutrient content, including fiber, ascorbic acid (vitamin C), potassium, and carotenoids (Andre et al., 2007; Burlingame et al., 2009). The nutritional diversity found in potato varieties is particularly evident in the Andes where mixtures are suggested to play an important role in dietary diversity (Picón-Reátegui, 1976). In this region, varieties can vary in concentrations of a given micronutrient by an order of magnitude and small portions of certain varieties can provide up to half of the daily required intake of a micronutrient, such as vitamin C (Andre et al., 2007).

We predict the greatest nutritional impact of varietal mixtures would be seen in subsistence or semi-subsistence agriculture systems where households predominantly consume crops they have grown or participate in local food supply chains. In these food systems, households could increase dietary diversity by expanding varietal diversity in their own fields or by purchasing food directly from local growers with diversified fields. Indeed, varietal mixtures are quite common in primarily subsistence agriculture systems where they are typically used to extend the harvest period and income generation, and curb crop disease (Smithson and Lenné, 1996). Whether these mixtures are currently planted with the explicit intent of increasing dietary diversity or the nutritional benefits are a “side-effect” of a strategy aimed primarily at providing other services, increasing awareness of the nutritional benefits associated with varietal mixtures could be particularly impactful for communities suffering from micronutrient deficiencies and would allow multiple services to be achieved simultaneously.

In contrast, we would expect fewer direct nutritional impacts of varietal mixtures in commercial food systems where the majority of households purchase food from retailers. Mainstream food supply chains provide a wide range of annual crop species and varieties,

regardless of whether the crops were grown in a monotypic or diversified field, as produce is pooled from multiple growers. However, a meaningful and growing number of households in the United States—where mainstream food supply chains are ubiquitous—are increasingly procuring produce from emerging food channels, such as community-supported agriculture (CSA), farmers markets, and farm stands (King et al., 2010). The nutritional benefits of varietal mixtures are more likely to emerge in these local food supply chains where households are purchasing directly from growers.

The extent of nutritional services provided by varietal mixtures will also vary depending on the crop species in question. For instance, we might expect varieties of vegetable and fruit crops that are directly consumed by humans to provide a greater nutritional impact than annual grain crops grown for human consumption, which often require processing. However, depending on the particular grain and type of processing, micronutrients can remain stable and, in some cases, become more concentrated during food processing (Slavin et al., 2000).

Given the wide range of nutrients found within a single crop species, the capacity to measure crop nutritional diversity has important implications for human health and nutrition, and deserves further attention (DeFries et al., 2015). To this end, we must transition from traditional yield- or calorie-based metrics to new metrics, such as nutritional functional diversity (FD), that consider the nutrient diversity of agroecosystems (Remans et al., 2011). Nutritional functional diversity (FD) was originally developed to describe the crop species composition in an agroecosystem as well as the nutritional composition of crops in terms of important nutrients, which are categorized as functional traits. In this context, functional diversity measures the variation in nutrient composition and content in a crop community (Remans et al., 2011). For example, incorporating a crop with a distinct nutrient profile would increase the nutritional functional diversity of a field. While the nutritional FD metric was originally developed to assess nutrient diversity at the species level, it could easily be extended to varietal mixtures as there is meaningful nutritional diversity to be leveraged within crop species (Andre et al., 2007; Broadley et al., 2007; Burlingame et al., 2009; George et al., 2004; Oury et al., 2006; Remans et

al., 2011). Indeed, measuring nutritional functional diversity could promote the use of varietal mixtures as a method for increasing dietary diversity, at little cost to growers, and would provide a more effective strategy for diversifying diets than randomly increasing the number of varieties in a mixture.

6. Conclusions

There is clear evidence that varietal mixtures are a feasible agricultural manipulation with the potential to support agroecosystem services that provide economic and nutritional benefits to humans (Fig. 1). Implementation of varietal mixtures seems quite viable in small markets dominated by farmers who are growing primarily for subsistence purposes, where changes to existing infrastructure and practices would be small in comparison to large-scale, conventional systems. However, with appropriate policy incentives, there is also potential for this practice to be adopted more widely in conventional agricultural systems, as has already been done for pathogen management in small grains (Finckh et al., 2000; Mundt, 2002; Tooker and Frank, 2012). Where marketing or processing requires the separation of varieties, varietal mixtures could be designed to accommodate mechanized equipment in the form of strip mixtures where the varieties are mixed in alternating strips of rows.

To expand the adoption of varietal mixtures, a number of knowledge gaps require attention. We lack a clear understanding of when and where the services provided by varietal mixtures are likely to be strongest in agroecosystems. For instance, we have yet to understand how a range of arthropod herbivores and natural enemies respond to this level of diversity (Tooker and Frank, 2012). Further research is also needed to determine how genetically diverse a varietal mixture needs to be to simultaneously support the ecological, nutritional, and economic components of agroecosystems, and whether or not this level of diversity is consistent across agricultural systems (e.g., primarily subsistence vs. commercial).

It is also imperative that we explore the mechanisms underlying the ecological impacts associated with varietal mixtures (Hughes et al., 2008). Understanding these mechanisms will

allow us to enhance agroecosystem services that support food security. Research in natural systems has highlighted the need to comprehensively compare the relative importance of interspecific and intraspecific plant diversity for ecological processes (Cook-Patton et al., 2011; Tooker and Frank, 2012); this knowledge would be particularly valuable in an agricultural context as it would expand management options for growers.

Understanding the effects of varietal mixtures on farm profitability under different management regimes is another key area of research that will help farmers design agroecosystems that capitalize on returns from ecosystem services. Implementing varietal mixtures may not require significant changes to existing management practices, but to understand whether or not this diversification strategy can benefit farmers, we need to accurately assess its effects on profitability through empirical economic analyses that measure both production costs and revenue generation, ideally over multiple years.

Given the importance of micronutrients in supporting human health and their interlinked roles in physiological functions (Frison et al., 2006), it is vital that agricultural interventions measure not only the yield capabilities of agroecosystems, but nutrient diversity as well. To address nutritional services, further research and outreach underscoring the capacity of varietal mixtures to support dietary diversity and human well-being is needed, as its value is often underappreciated. For instance, in some regions where nutrient-related diseases remain common, intraspecific variation in nutrient content is not routinely considered to be an important characteristic when extension agents recommend cultivars to farmers (Huang et al., 1999; Toledo and Burlingame, 2006). The nutritional functional diversity metric is one tool that can address this issue by providing another dimension by which we can measure cultivar characteristics (Remans et al., 2011). By moving beyond the ecological aspects of functional diversity, this metric allows us to broaden our perspective on the functional capacity of agroecosystems.

As we seek to fill these knowledge gaps, we cannot focus our attention solely on varietal diversity per se, as the composition and functional diversity of varietal mixtures are likely to be significant drivers of agroecosystem processes (Gallandt et al., 2001; Mille et al., 2006; Newton

et al., 1997). To better understand the linkages between agrobiodiversity, resilient agroecosystems, and human nutrition, we need to simultaneously explore impacts on multiple outcomes, such as ecosystem services, dietary diversity, labor productivity, and livelihood status. Studies integrating agroecology, socioeconomics, and nutrition will guide us towards multi-functional, sustainable food systems.

Acknowledgements

The authors are grateful to L. Figueroa, A. Iverson, E. Lombardi, R. Nelson, R. Perez-Alvarez, J. Peters, K. Poveda, and J. Thaler for discussion and helpful comments. LS was supported by the National Science Foundation (NSF) through a Graduate Research Fellowship and the Food Systems and Poverty Reduction Integrative Graduate Education and Research Traineeship at Cornell University (#DGE-0903371). AP received support from Cornell University, USDA-NIFA AFRI Grant #2013-67013-21235, and the Collaborative Crop Research Program of the McKnight Foundation.

REFERENCES

- Altieri, M.A., 1999. The ecological role of biodiversity in agroecosystems. *Agric. Ecosyst. Environ.* 74, 19–31. [https://doi.org/10.1016/S0167-8809\(99\)00028-6](https://doi.org/10.1016/S0167-8809(99)00028-6)
- Andow, D. a, 1991. Vegetational diversity and arthropod population response. *Rev. Entomol* 36, 561–6. <https://doi.org/10.1146/annurev.en.36.010191.003021>
- Andre, C.M., Ghislain, M., Bertin, P., Oufir, M., del Rosario Herrera, M., Hoffman, L., Hausman, J.F., Larondelle, Y., Evers, D., 2007. Andean Potato Cultivars (*Solanum tuberosum* L.) as a Source of Antioxidant and Mineral Micronutrients. *J. Agric. Food Chem.* 55, 366–378. <https://doi.org/10.1021/jf062740i>
- Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A., Szendrei, Z., 2009. Associational Resistance and Associational Susceptibility: Having Right or Wrong Neighbors. *Annu. Rev. Ecol. Evol. Syst.* 40, 1–20. <https://doi.org/10.1146/annurev.ecolsys.110308.120242>
- Barot, S., Allard, V., Cantarel, A., Enjalbert, J., Gauffreteau, A., Goldringer, I., Lata, J.C., Le Roux, X., Niboyet, A., Porcher, E., 2017. Designing mixtures of varieties for multifunctional agriculture with the help of ecology. A review. *Agron. Sustain. Dev.* 37. <https://doi.org/10.1007/s13593-017-0418-x>
- Belloti, A., Herrera Campo, B. V., Hyman, G., 2012. Cassava production and pest management: Present and potential threats in a changing environment. *Trop. Plant Biol.* 5, 39–72.
- Bianchi, F.J.J.A., Booij, C.J.H., Tschardtke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. Biol. Sci.* 273, 1715–1727. <https://doi.org/10.1098/rspb.2006.3530>
- Brier, H.B., Murray, D.A.H., Wilson, L.J., Nicholas, A.H., Miles, M.M., Grundy, P.R., McLennan, A.J., 2008. An overview of integrated pest management (IPM) in north-eastern Australian grain farming systems: Past, present and future prospects. *Aust. J. Exp. Agric.* 48, 1574–1593. <https://doi.org/10.1071/EA08166>

- Broadley, M., Meacham, M., Bowen, H., Hammond, J., Hyden, R., Mead, A., Teakle, G., King, G., White, P., 2007. Natural genetic variation in the mineral nutrient composition of *Brassica oleracea*. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* 146, S246–S247. <https://doi.org/10.1016/j.cbpa.2007.01.570>
- Bullock, J.M., Dhanjal-Adams, K.L., Milne, A., Oliver, T.H., Todman, L.C., Whitmore, A.P., Pywell, R.F., 2017. Resilience and food security: rethinking an ecological concept. *J. Ecol.* 105, 880–884. <https://doi.org/10.1111/1365-2745.12791>
- Burlingame, B., Mouille, B., Charrondiere, R., 2009. Nutrients, bioactive non-nutrients and anti-nutrients in potatoes. *J. Food Compos. Anal.* 22, 494–502. <https://doi.org/10.1016/j.jfca.2009.09.001>
- Chavas, J.P., Di Falco, S., 2012. On the role of risk versus economies of scope in farm diversification with an application to ethiopian farms. *J. Agric. Econ.* 63, 25–55. <https://doi.org/10.1111/j.1477-9552.2011.00319.x>
- Clawson, D.L., 1985. Harvest Security and Intraspecific Diversity in Traditional Tropical Agriculture 39, 56–67.
- Cook-Patton, S.C., McArt, S.H., Parachnowitsch, A.L., Thaler, J.S., Agrawal, A.A., 2011. A direct comparison of the consequences of plant genotypic and species diversity on communities and ecosystem function. *Ecology* 92, 915–23.
- Cowger, C., Weisz, R., 2008. Winter wheat blends (mixtures) produce a yield advantage in North Carolina. *Agron. J.* 100, 169–177. <https://doi.org/10.2134/agronj2007.0128>
- Dahlin, I., Rubene, D., Glinwood, R., Ninkovic, V., 2018. Pest suppression in cultivar mixtures is influenced by neighbor-specific plant – plant communication. *Ecol. Appl.* 28, 2187–2196. <https://doi.org/10.1002/eap.1807>
- DeFries, R., Fanzo, J., Remans, R., Palm.Cheryl, Wood, S., Anderman, T.L., 2015. Metrics for land-scarce agriculture. *Science.* 349, 238–240.

- Dogimont, C., Bendahmane, A., Pitrat, M., Burget-Bigeard, E., Hagen, L., Le Menn, A., Pauquet, J., Rousselle, P., Caboche, M., Chovelon, V., 2009. Gene resistance to *Aphis gossypii*. 0070016977.
- Döring, T.F., Vieweger, A., Pautasso, M., Vaarst, M., Finckh, M.R., Wolfe, M.S., 2015. Resilience as a universal criterion of health. *J. Sci. Food Agric.* 95, 455–465. <https://doi.org/10.1002/jsfa.6539>
- Dutcher, J.D., 2007. A review of resurgence and replacement causing pest outbreaks in IPM. *Gen. Concepts Integr. Pest Dis. Manag.* 27–43. https://doi.org/10.1007/978-1-4020-6061-8_2
- Esquinas-Alcazar, J., 2005. Protecting crop genetic diversity for food security: political, ethical and technical challenges. *Nat Rev Genet* 6, 946–953.
- FAO, 2015. “FAOSTAT.” Rome, Italy.
- Finckh, M.R., Gacek, E.S., Goyeau, H., Lannou, C., Merz, U., Mundt, C.C., Munk, L., Nadziak, J., Newton, A.C., de Vallavieille-Pope, C., Wolfe, M.S., 2000. Cereal variety and species mixtures in practice, with emphasis on disease resistance. *Agronomie* 20, 813–837. <https://doi.org/10.1051/agro:2000177>
- Food and agriculture Organization of the United Nations, R., 2010. The State of Food Insecurity in the World Addressing food insecurity in protracted crises 2010 Key messages, Notes.
- Frison, E., Smith, I.F., Johns, T., Cherfas, J., Eyzaguirre, P.B., 2006. Agricultural Diversity, Nutrition, and Health : Making a Difference to Hunger and Nutrition in the Developing World. *Food Nutr. Bull.* 27, 167–179. <https://doi.org/10.1177/156482650602700208>
- Gallai, N., Salles, J.M., Settele, J., Vaissière, B.E., 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol. Econ.* 68, 810–821. <https://doi.org/10.1016/j.ecolecon.2008.06.014>
- Gallandt, E.R., Dofing, S.M., Reisenauer, P.E., Donaldson, E., 2001. Diallel analysis of cultivar mixtures in winter wheat. *Crop Sci.* 41, 792–796.

- Gallun, R.L., 1977. Genetic basis of Hessian fly epidemics. *Ann. N. Y. Acad. Sci.* 287, 223–229.
<https://doi.org/10.1111/j.1749-6632.1977.tb34241.x>
- Garibaldi, L.A., Aizen, M.A., Klein, A.M., Cunningham, S.A., Harder, L.D., 2011. Global growth and stability of agricultural yield decrease with pollinator dependence. *Proc. Natl. Acad. Sci. U. S. A.* 108, 5909–14. <https://doi.org/10.1073/pnas.1012431108>
- Gaudin, A.C., M., Tolhurst, T.N., Ker, A.P., Janovicek, K., Tortora, C., Martin, R.C., Deen, W., 2015. Increasing crop diversity mitigates weather variations and improves yield stability. *PLoS One* 10, 1–21. <https://doi.org/10.1371/journal.pone.0113261>
- Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tschardt, T., Winqvist, C., Eggers, S., Bommarco, R., Part, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Onate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hanke, S., Fischer, C., Goedhart, P.W., Inchausti, P., 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic Appl. Ecol.* 11, 97–105. <https://doi.org/10.1016/j.baae.2009.12.001>
- George, B., Kaur, C., Khurdiya, D.S., Kapoor, H.C., 2004. Antioxidants in tomato (*Lycopersium esculentum*) as a function of genotype. *Food Chem.* 84, 45–51.
[https://doi.org/10.1016/S0308-8146\(03\)00165-1](https://doi.org/10.1016/S0308-8146(03)00165-1)
- Gibbs, K.E., MacKey, R.L., Currie, D.J., 2009. Human land use, agriculture, pesticides and losses of imperiled species. *Divers. Distrib.* 15, 242–253. <https://doi.org/10.1111/j.1472-4642.2008.00543.x>
- Gliessman, S., 1985. Multiple Cropping Systems: A Basis for Developing an Alternative Agriculture, in: *Innovative Technologies for Lesser Developed Countries*. pp. 69–86.
- Graham, R.D., Welch, R.M., Saunders, D.A., Ortiz-Monasterio, I., Bouis, H.E., Bonierbale, M., de Haan, S., Burgos, G., Thiele, G., Liria, R., Meisner, C. a., Beebe, S.E., Potts, M.J., Kadian, M., Hobbs, P.R., Gupta, R.K., Twomlow, S., 2007. Nutritious Subsistence Food Systems. *Adv. Agron.* 92, 1–74. [https://doi.org/10.1016/S0065-2113\(04\)92001-9](https://doi.org/10.1016/S0065-2113(04)92001-9)

- Grusak, M.A., DellaPenna, D., 1999. Improving the Nutrient Composition of Plants To Enhance Human Nutrition and Health¹. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 50, 133–161. <https://doi.org/10.1146/annurev.arplant.50.1.133>
- Gurr, G.M., Wratten, S.D., Altieri, M.A., 2004. Ecological Engineering for Pest Management. *Plant Prot. Q.* 30, 244. <https://doi.org/10.1111/j.1442-9993.2005.01456.x>
- Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Knops, J.M.H., Tilman, D., 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecol. Lett.* 12, 1029–1039. <https://doi.org/10.1111/j.1461-0248.2009.01356.x>
- Hahlbrock, K., Scheel, D., 1989. Physiology and molecular biology of phenylpropanoid metabolism. *Annu. Rev. Plant Physiol.* 40, 347–69.
- Hall, A.E., Patel, P.N., 1985. Cowpea breeding for resistance to drought and heat, in: Singh, S.R., Rachie, K.O. (Eds.), *Cowpea Research, Production, and Utilization*. John Wiley & Sons, New York, pp. 137–151.
- Harrison, K.A., Bol, R., Bardgett, R.D., 2008. Do plant species with different growth strategies vary in their ability to compete with soil microbes for chemical forms of nitrogen? *Soil Biol. Biochem.* 40, 228–237. <https://doi.org/10.1016/j.soilbio.2007.08.004>
- Herforth, A., Jones, A., Pinstrip-Andersen, P., 2012. Prioritizing nutrition in agriculture and rural development, HNP Discussion Papers Series. Washington, D.C. <https://doi.org/10.13140/RG.2.1.4798.1521>
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol. Monogr.* 75, 3–35. <https://doi.org/10.1890/04-0922>
- Huang, A.S., Tanudjaja, L., Lum, D., 1999. Content of Alpha- , Beta-Carotene , and Dietary Fiber in 18 Sweetpotato Varieties Grown in Hawaii. *J. Food Compos. Anal.* 151, 147–151.

- Hughes, A.R., Inouye, B.D., Johnson, M.T.J., Underwood, N., Vellend, M., 2008. Ecological consequences of genetic diversity. *Ecol. Lett.* 11, 609–23. <https://doi.org/10.1111/j.1461-0248.2008.01179.x>
- Huston, M.A., 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110, 449–460.
- IFPRI, 2014. Global Nutrition Report 2014: Actions and accountability to accelerate the world’s progress on nutrition. Washington, D.C.
- Iverson, A.L., Marin, L.E., Ennis, K.K., Gonthier, D.J., Connor-Barrie, B.T., Remfert, J.L., Cardinale, B.J., Perfecto, I., 2014. Do polycultures promote win-wins or trade-offs in agricultural ecosystem services? A meta-analysis. *J. Appl. Ecol.* 51, 1593–1602. <https://doi.org/10.1111/1365-2664.12334>
- Johns, T., Eyzaguirre, P.B., 2006. Linking biodiversity, diet and health in policy and practice. *Proc. Nutr. Soc.* 65, 182–189. <https://doi.org/10.1079/PNS2006494>
- Johnson, I.T., 2002. Glucosinolates in the human diet. Bioavailability and implications for health. *Phytochem. Rev.* 1, 183–188.
- Karp, D.S., Rominger, A.J., Zook, J., Ranganathan, J., Ehrlich, P.R., Daily, G.C., 2012. Intensive agriculture erodes β -diversity at large scales. *Ecol. Lett.* 15, 963–970. <https://doi.org/10.1111/j.1461-0248.2012.01815.x>
- Kaut, A.H.E.E., Mason, H.E., Navabi, A., O’Donovan, J.T., Spaner, D., 2009. Performance and stability of performance of spring wheat variety mixtures in organic and conventional management systems in western Canada. *J. Agric. Sci.* 147, 141. <https://doi.org/10.1017/S0021859608008319>
- Khan, Z.R., Midega, C.A.O., Amudavi, D.M., Hassanali, A., Pickett, J.A., 2008. On-farm evaluation of the “push-pull” technology for the control of stemborers and striga weed on maize in western Kenya. *F. Crop. Res.* 106, 224–233. <https://doi.org/10.1016/j.fcr.2007.12.002>

- King, R.P., Hand, M.S., Digiacomio, G., Clancy, K., Gómez, M.I., Hardesty, S.D., Lev, L., Mclaughlin, E.W., 2010. Comparing the Structure, Size, and Performance of Local and Mainstream Food Supply Chains, ERR-99.
- Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. Biol. Sci.* 274, 66, 95–96, 191. <https://doi.org/10.1098/rspb.2006.3721>
- Koricheva, J., Hayes, D., 2018. The relative importance of plant intraspecific diversity in structuring arthropod communities: a meta-analysis. *Funct. Ecol.* 1–14. <https://doi.org/10.1111/1365-2435.13062>
- Letourneau, D.K., Ambrecht, I., Rivera, B.S., Lerma, J.M., Carmona, E.J., Daza, M.C., Escobar, S., Galindo, V., Gutiérrez, C., López, S.D., Mejía, J.L., Rangel, A.M.A., Rangel, J.H., Rivera, L., Saavedra, C.A., Torres, A.M., Trujillo, A.R., 2011. Does plant diversity benefit agroecosystems? A synthetic review. *Ecol. Appl.* 21, 9–21.
- Lin, B.B., 2011. Resilience in Agriculture through Crop Diversification: Adaptive Management for Environmental Change. *Bioscience* 61, 183–193. <https://doi.org/10.1525/bio.2011.61.3.4>
- Lin, B.B., Perfecto, I., Vandermeer, J., 2008. Synergies between Agricultural Intensification and Climate Change Could Create Surprising Vulnerabilities for Crops. *Bioscience* 58, 847. <https://doi.org/10.1641/B580911>
- Loreau, M., 2000. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* 91, 3–17.
- Loreau, M., Hector., 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412, 72–6. <https://doi.org/10.1038/35083573>
- Lupton, F.G.H., Olover, R.H., Ellis, F.B., Barnes, B.T., Howse, K.R., Welbank, P.J., Taylor, P.J., 1974. Root and shoot growth of semi-dwarf and taller winter wheats. *Ann. Appl. Biol.* 77, 129–144. <https://doi.org/10.1111/j.1744-7348.1974.tb06881.x>

- McIntyre, B., Herre, H.R., Wakhungu, J., Watson, R.T. (Eds.), 2009. International assessment of agricultural knowledge, science and technology for development. Island Press, Washington, D.C.
- Meehan, T.D., Werling, B.P., Landis, D.A., Gratton, C., 2011. Agricultural landscape simplification and insecticide use in the Midwestern United States. *Proc. Natl. Acad. Sci.* 108, 11500–11505. <https://doi.org/10.1073/pnas.1100751108>
- Mille, B., Belhaj Fraj, M., Monod, H., De Vallavieille-Pope, C., 2006. Assessing four-way mixtures of winter wheat cultivars from the performances of their two-way and individual components. *Eur. J. Plant Pathol.* 114, 163–173. <https://doi.org/10.1007/s10658-005-4036-0>
- Mundt, C.C., 2002. Use of multiline cultivars and cultivar mixtures for disease management. *Annu. Rev. Phytopathol.* 40, 381–410. <https://doi.org/10.1146/annurev.phyto.40.011402.113723>
- Murray, D.A.H., Miles, M.M., McLennan, A.J., Lloyd, R.J., Hopkinson, J.E., 2005. Area-wide management of *Helicoverpa* spp. in an Australian mixed cropping agroecosystem, in: *Proceedings of the 2005 Beltwide Cotton Conference*. New Orleans.
- Negin, J., Remans, R., Karuti, S., Fanzo, J.C., 2009. Integrating a broader notion of food security and gender empowerment into the African Green Revolution. *Food Secur.* 1, 351–360. <https://doi.org/10.1007/s12571-009-0025-z>
- Newton, A.C., Ellis, R.P., Hackett, C.A., Guy, D.C., 1997. The effect of component number on *Rhynchosporium secalis* infection and yield in mixtures of winter barley cultivars. *Plant Pathol.* 46, 930–938. <https://doi.org/10.1046/j.1365-3059.1997.d01-83.x>
- Ninkovic, V., 2003. Volatile communication between barley plants affects biomass allocation. *J. Exp. Bot.* 54, 1931–1939. <https://doi.org/10.1093/jxb/erg192>
- Nombela, G., Williamson, V.M., Muñoz, M., 2003. The root-knot nematode resistance gene Mi-1.2 of tomato is responsible for resistance against the whitefly *Bemisia tabaci*. *Mol. Plant. Microbe. Interact.* 16, 645–649. <https://doi.org/10.1094/MPMI.2003.16.7.645>

- Oury, F.X., Leenhardt, F., Rémésy, C., Chanliaud, E., Duperrier, B., Balfourier, F., Charmet, G., 2006. Genetic variability and stability of grain magnesium, zinc and iron concentrations in bread wheat. *Eur. J. Agron.* 25, 177–185. <https://doi.org/10.1016/j.eja.2006.04.011>
- Peacock, L., Herrick, S., 2000. Responses of the willow beetle *Phratora vulgatissima* to genetically and spatially diverse *Salix* spp. plantations. *J. Appl. Ecol.* 37, 821–831. <https://doi.org/10.1046/j.1365-2664.2000.00528.x>
- Peltonen-Sainio, P., Karjalainen, R., 1991. Agronomic evaluation of growing oat cultivar mixtures under various stress conditions in Finland. *Acta Agric. Scand.* 41, 47–53. <https://doi.org/10.1080/00015129109438582>
- Peterson, J.A., Ode, P.J., Oliveira-hofman, C., Harwood, J.D., Brennan, R., Birch, A.N., 2016. Integration of Plant Defense Traits with Biological Control of Arthropod Pests: Challenges and Opportunities. *Front. Plant Sci.* 7, 1–23. <https://doi.org/10.3389/fpls.2016.01794>
- Picón-Reátegui, E., 1976. Nutrition. In *man in the Andes*. Dowden, Hutchinson and Ross, Stroudsburg, PA.
- Pingali, P.L., 2012. Green Revolution: Impacts, limits, and the path ahead. *PNAS* 109, 12302–12308. <https://doi.org/10.1073/pnas.0912953109>
- Poveda, K., Gomez, M., Martinez, E., 2008. Diversification practices: their effect on pest regulation and production. *Rev. Colomb. Entomol.* 34, 131–144.
- Power, A.G., 2010. Ecosystem services and agriculture: tradeoffs and synergies. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 365, 2959–2971. <https://doi.org/10.1098/rstb.2010.0143>
- Power, A.G., 1991. Virus spread and vector dynamics in genetically diverse plant populations. *Ecology* 72, 232–241.
- Prasad, A.S., 1998. Zinc in human health: An update. *J. Trace Elem. Exp. Med.* 11, 63–87.
- Pring, D.R., Lonsdale, D.M., 1989. Cytoplasmic Male Sterility and Maternal Inheritance of Disease Susceptibility in Maize. *Annu. Rev. Phytopathol.* 27, 483–502. <https://doi.org/10.1146/annurev.py.27.090189.002411>

- Rasmann, S., Kollner, T.G., Degenhardt, J., Hiltbold, I., Toepfer, S., Kuhlmann, U., Gershenzon, J., Turlings, T.C.J., 2005. Recruitment of entomopathogenic nematodes by insect-damaged maize roots. *Nature* 434, 732–737.
- Reiss, E.R., Drinkwater, L.E., 2018. Cultivar mixtures: A meta-analysis of the effect of intraspecific diversity on crop yield: *A. Ecol. Appl.* 28, 62–77.
<https://doi.org/10.1002/eap.1629>
- Remans, R., Flynn, D.F.B., DeClerck, F., Diru, W., Fanzo, J., Gaynor, K., Lambrecht, I., Mudiope, J., Mutuo, P.K., Nkhoma, P., Siriri, D., Sullivan, C., Palm, C.A., 2011. Assessing nutritional diversity of cropping systems in African villages. *PLoS One* 6, e21235. <https://doi.org/10.1371/journal.pone.0021235>
- Reynolds, H.L., Packer, A., Bever, J.D., Clay, K., 2003. Grassroots Ecology: Plant – Microbe – Soil Interactions As Drivers of Plant Community Structure and Dynamics. *Ecology* 84, 2281–2291. <https://doi.org/10.1890/02-0298>
- Ricketts, T.H., Daily, G.C., Ehrlich, P.R., Michener, C.D., 2004. Economic value of tropical forest to coffee production. *Proc. Natl. Acad. Sci. U. S. A.* 101, 12579–82.
<https://doi.org/10.1073/pnas.0405147101>
- Root, R.B., 1973. Organization of a Plant-Arthropod Association in Simple and Diverse Habitats: The Fauna of Collards (*Brassica Oleracea*). *Ecol. Monogr.* 43, 95–124.
- Rossi, M., Goggin, F.L., Milligan, S.B., Kaloshian, I., Ullman, D.E., Williamson, V.M., 1998. The nematode resistance gene *Mi* of tomato confers resistance against the potato aphid. *Pnas* 95, 9750–9754. <https://doi.org/10.1073/pnas.95.17.9750>
- Sarandon, S.J., Sarandon, R., 1995. Mixture of Cultivars - Pilot Field Trial of an Ecological Alternative to Improve Production or Quality of Wheat (*Triticum-Aestivum*). *J. Appl. Ecol.* 32, 288–294. <https://doi.org/10.2307/2405096>
- Schellhorn, N.A., Parry, H.R., Macfadyen, S., Wang, Y., Zalucki, M.P., 2015. Connecting scales: Achieving in-field pest control from areawide and landscape ecology studies. *Insect Sci.* 22, 35–51. <https://doi.org/10.1111/1744-7917.12161>

- Sessitsch, A., Reiter, B., Pfeifer, U., Wilhelm, E., 2002. Cultivation-independent population analysis of bacterial endophytes in three potato varieties based on eubacterial and Actinomycetes -specific PCR of 16S rRNA genes. *FEMS Microbiol. Ecol.* 39, 23–32.
- Slavin, J.L., Jacobs, D., Marquart, L., 2000. Grain Processing and Nutrition. *Crit. Rev. Food Sci. Nutr.* 40, 309–326. <https://doi.org/10.1080/10408690091189176>
- Smirnoff, N., 1996. The Function and Metabolism of Ascorbic Acid in Plants. *Ann. Bot.* 78, 661–669. <https://doi.org/10.1006/anbo.1996.0175>
- Smithson, J.B., Lenné, J.M., 1996. Varietal mixtures: a viable strategy for sustainable productivity in subsistence agriculture. *Ann. Appl. Biol.* 128, 127–158. <https://doi.org/10.1111/j.1744-7348.1996.tb07096.x>
- Tahvanainen, J.O., Root, R.B., 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* 10, 321–346.
- Talalay, P., Fahey, J.W., 2001. Phytochemicals from cruciferous plants protect against cancer by modulating carcinogen metabolism. *J. Nutr.* 131, 3027S–33S.
- Thiaw, S., Hall, A.E., Parker, D.R., 1993. Varietal intercropping and the yields and stability of cowpea production in semiarid Senegal. *F. Crop. Res.* 33, 217–233.
- Thies, C., Steffan-Dewenter, I., Tschardt, T., 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos* 101, 18–25. <https://doi.org/10.1034/j.1600-0706.2003.12567.x>
- Thrupp, L.A., 2000. Linking Agricultural Biodiversity and Food Security: The Valuable Role of Sustainable Agriculture. *Int. Aff.* 76, 265–281.
- Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., Polasky, S., Chikowo, R., Corbeels, M., Tittone, P., Vanlauwe, B., Whitbread, A., Giller, K.E., Cossio, M.L.T., Giesen, L.F., Araya, G., Pérez-Cotapos, M.L.S., VERGARA, R.L., Manca, M., Tohme, R.A., Holmberg, S.D., Bressmann, T., Lirio, D.R., Román, J.S., Solís, R.G., Thakur, S., Rao, S.N., Modelado, E.L., La, A.D.E., Durante, C., Tradición, U.N.A., En, M., Espejo, E.L.,

- Fuentes, D.E.L.A.S., Yucatán, U.A. De, Lenin, C.M., Cian, L.F., Douglas, M.J., Plata, L., Hérítier, F., Tanaka, D.L., Krupinsky, J.M., Liebig, M. a., Merrill, S.D., Ries, R.E., Hendrickson, J.R., Johnson, H. a., Hanson, J.D., Morison, J.I., Baker, N., Mullineaux, P., Davies, W., Sinclair, T.R., Tanner, C.B., Bennett, J.M., Brigitte Baptiste, B.M.-L., Zhang, F., Li, L., 2002. Agriculture Sustainability and Intensive Production Practices. *Nature* 418, 671–677. <https://doi.org/10.1007/s13398-014-0173-7.2>
- Tilman, D., Tilman, D., Lehman, C.L., Lehman, C.L., Thomson, K.T., Thomson, K.T., 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl. Acad. Sci. U. S. A.* 94, 1857–61. <https://doi.org/10.1073/pnas.94.5.1857>
- Toledo, Á., Burlingame, B., 2006. Biodiversity and nutrition: A common path toward global food security and sustainable development. *J. Food Compos. Anal.* 19, 477–483. <https://doi.org/10.1016/j.jfca.2006.05.001>
- Tooker, J.F., Frank, S.D., 2012. Genotypically diverse cultivar mixtures for insect pest management and increased crop yields. *J. Appl. Ecol.* <https://doi.org/10.1111/j.1365-2664.2012.02173.x>
- Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012a. Global food security, biodiversity conservation and the future of agricultural intensification. *Biol. Conserv.* 151, 53–59. <https://doi.org/10.1016/j.biocon.2012.01.068>
- Tscharntke, T., Tylianakis, J.M., Rand, T. a., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D. a., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012b. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev.* 87, 661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>
- Ugent, D., 1968. The Potato in Mexico: Geography and Primitive Culture. *Econ. Bot.* 22, 108–123.

- Underwood, N., 2004. Variance and skew of the distribution of plant quality influence herbivore population dynamics. *Ecology* 85, 686–693.
- Wetzel, W.C., Kharouba, H.M., Robinson, M., Holyoak, M., Karban, R., 2016. Variability in plant nutrients reduces insect herbivore performance. *Nature* 539, 425–427.
- Wilhoit, L.R., 1992. Evolution of herbivore virulence to plant resistance: influence of variety mixtures, in: Fritz, R.S., Simms, E.L. (Eds.), *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution and Genetics*. University of Chicago Press, Chicago, pp. 91–119.
- Wolfe, M.S., 1985. Prospects of Multiline Mixtures for Disease. *Annu. Rev. Phytopathol.* 23, 251–273. <https://doi.org/10.1146/annurev.py.23.090185.001343>
- Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci. U. S. A.* 96, 1463–1468. <https://doi.org/10.1073/pnas.96.4.1463>
- Zhu, Y., Chen, H., Fan, J., Wang, Y., Li, Y., Chen, J., Yang, S., Hu, L., Leung, H., Mew, T.W., Teng, P.S., Wang, Z., Mundt, C.C., 2000. Genetic diversity and disease control in rice. *Nature* 406, 718–22. <https://doi.org/10.1038/35021046>
- Zuppinger-Dingley, D., Schmid, B., Petermann, J.S., Yadav, V., Deyn, G.B. De, Flynn, D.F.B., 2014. Selection for niche differentiation in plant. *Nature* 515, 108–111. <https://doi.org/10.1038/nature13869>

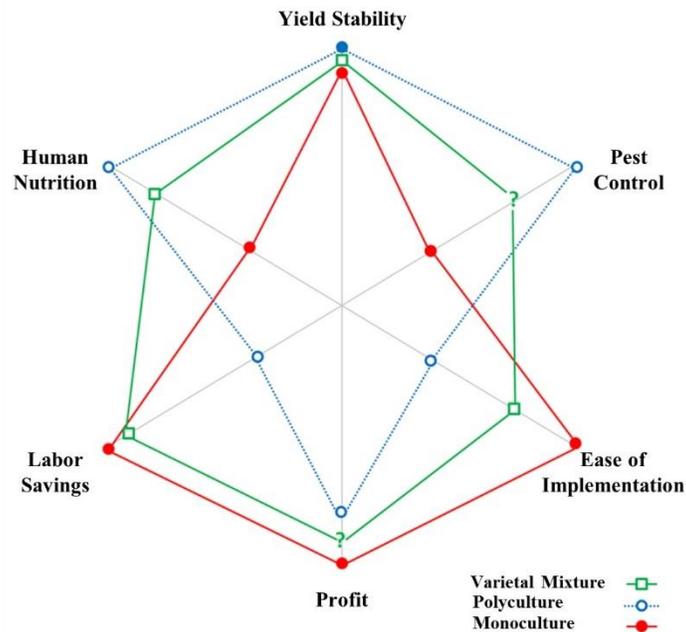


Figure 1.1. Conceptual framework for comparing the services (human nutrition, yield stability, pest control) and economic implications (labor, implementation effort, profits) associated with agricultural management practices. In this qualitative diagram, the level of service or economic implication is indicated along each axis; achieving greater distance along each axis indicates a stronger benefit. We compare services and economic implications across three hypothetical agriculture systems: a monoculture (closed circle), a polyculture (open circle), and a varietal mixture (open square). In general, polycultures enhance many services, but production costs can be high. In contrast, monocultures minimize costs, but are poor producers of services. We propose that varietal mixtures could serve as an intermediate strategy. The symbol ‘?’ represents predictions with the least amount of supporting evidence.

CHAPTER TWO

LANDSCAPE-DEPENDENT EFFECTS OF VARIETAL MIXTURES ON INSECT PEST CONTROL AND IMPLICATIONS FOR FARMER PROFITS

Lauren D. Snyder, Miguel I. Gómez, Erika L. Mudrak, and Alison G. Power

Abstract

Intraspecific plant diversity can significantly impact insect herbivore populations in unmanaged ecosystems. Yet, its role as an insect pest control strategy in agricultural systems has received less attention, and little is known about which crop traits are important to herbivores in different landscape contexts. Moreover, empirical economic analyses on the cost-effectiveness of this management practice are lacking. We used varietal mixtures of *Brassica oleracea* crops on working farms to examine how two metrics of intraspecific crop diversity—varietal richness and number of plant colors (color richness)—affect crop damage and the incidence and abundance of two insect pests, *Pieris rapae* and *Phyllotreta* spp. We evaluated the context-dependency of varietal mixtures by sampling early and late season plantings of *B. oleracea* crops in farms across a gradient of landscape composition. We developed crop budgets and used a net present value analysis to assess the impact of varietal mixtures on input and labor costs, crop revenues, and profit. We found context-dependent effects of varietal mixtures on both pests. Color richness had no effect on *Phyllotreta* spp. populations in early season plantings. Increasing varietal richness reduced *Phyllotreta* spp. incidence in simple landscapes dominated by croplands, but this trend was reversed in complex landscapes dominated by natural habitats. In contrast, in late season plantings, increasing varietal and color richness reduced the incidence and abundance of *P. rapae* larvae, but only in complex landscapes where their populations were highest. Unexpectedly, we consistently found lower pest pressure and reduced crop damage in simple landscapes. Although varietal mixtures did not affect crop damage, increasing color richness was associated with increased profits, due to increased revenue and a marginal reduction in labor and input costs. We demonstrate that varietal mixtures can have significant impacts on pest

populations, and that this effect can be mediated by intraspecific variation in crop traits. However, the strength and direction of these effects vary by season, landscape composition, and pest species. The association between varietal color richness and profitability indicates that farmers could design mixtures to enhance economic returns. We recommend additional research on the potential benefits of intraspecific trait variation for farmers.

Introduction

Low-diversity intensified agricultural systems have been implemented on a global scale in an effort to produce sufficient food for a growing human population. Although these systems can be highly productive in combination with external inputs, valuable ecosystem services such as pest control are often not supported (Altieri 1999, Power 2010). Increasing crop species diversity in the form of polycultures is an agroecological strategy long used by smallholder farmers around the world, and a strong body of literature shows polycultures support pest control services (reviewed in Andow, 1991; Letourneau et al., 2011). This service may be driven by natural enemies or by multiple characteristics of crop species diversity, such as increased color, chemical, or structural variation (Cartea et al. 2010), which can diminish herbivores' ability to locate preferred host plants, as suggested by the resource concentration hypothesis (Root 1973). However, despite potential pest control services and other benefits, polycultures can be costly. For instance, polycultures may not lend themselves to mechanized agricultural equipment, thereby increasing labor requirements, and they demand more agronomic knowledge than monocultures because growers must be familiar with the planting times, management needs, and marketability of each crop species (Gliessman, 1985).

A growing body of research suggests that intraspecific plant diversity—genetic diversity within a plant species—may be as important in structuring insect communities as plant species diversity (Crawford & Rudgers, 2013; reviewed in Tooker & Frank, 2012). For some farmers, increasing crop diversity in the form of varietal mixtures may be a more feasible management practice than polycultures because they require relatively minor changes to agricultural practices

(Tooker and Frank 2012). For instance, farmers could expand varietal diversity in a crop species they already grow, thus providing a less costly diversification strategy. The potential for varietal mixtures to provide a less labor-intensive diversification strategy is particularly appealing, because labor is often the most expensive and difficult input for growers to procure (Bronars 2014, Duvall 2017). However, there are few studies evaluating the impact of varietal mixtures on labor costs and grower profits, which impedes our ability to provide effective recommendations to growers.

Despite long-standing use of varietal mixtures for pathogen control in cereal crops and considerable interest in using them for insect pest control, most studies exploring the effect of varietal mixtures on insects have been carried out in natural systems, with fewer studies in agricultural systems (reviewed in Tooker & Frank, 2012). Furthermore, most of the studies in agricultural systems have focused on whether the effects of varietal mixtures exist, and there has been less emphasis on understanding which functional traits present in crop mixtures influence insect communities in the field. Studies from natural systems indicate that insect pests respond to intraspecific variation in morphological plant traits, such as leaf color, in genotypic mixtures (Sinkkonen et al. 2012, Green et al. 2015). However, the effect of intraspecific trait variation in crop varietal mixtures on agricultural insect pests is poorly understood.

Some studies in agricultural systems have shown a strong effect of varietal mixtures on insect populations (Altieri and Schmidt 1987, Power 1988), while others have shown little or no effect (Cantelo and Sanford 1984, Power 1988). We suggest the mixed results from these studies could be related to spatial and temporal variation in the dynamics of insect pests and their natural enemies. For example, landscape composition is known to strongly influence insect populations (Bianchi et al. 2006, Tscharntke et al. 2007) and the effectiveness of management practices at the local-scale (Tscharntke et al. 2012). Landscapes with a high proportion of natural areas are frequently associated with high natural enemy abundance, which in turn can enhance pest control services (Gardiner et al. 2009, Chaplin-Kramer et al. 2011). Measuring temporal dynamics is also important because pest and natural enemy populations, along with crop damage, fluctuate

over a growing season (Chaplin-Kramer et al. 2013). For example, in brassica crops grown in central NY State, flea beetles (*Phyllotreta* spp.) are the primary insect pests in the early growing season (April-June), while the small white butterfly (*Pieris rapae*) becomes a dominant pest in the late growing season (June-August) (Seaman 2013). Therefore, the effectiveness of varietal mixtures as a pest management strategy is likely to vary across time and space. While previous field studies on varietal mixtures have accounted for temporal variation by sampling pests throughout a growing season, little is known about the interaction between varietal mixtures and landscape composition.

Here, we evaluate the effects of early and late season plantings of *Brassica oleracea* mixtures (local-scale intraspecific crop diversity) and the percent of cropland at the landscape-scale on the incidence and abundance of two important cruciferous pests—*P. rapae* and flea beetles—and resulting crop damage. In addition, we explore the role of an important crop trait, varietal color, in mediating these services. While *B. oleracea* varieties vary in a number of functional traits, such as plant structure and phytochemical composition, in this study we focus on intraspecific variation in plant color for several reasons 1) cruciferous herbivores are known to use color as a visual cue in host selection (Yang et al. 2003, Tsuji and Coe 2014), 2) color is correlated with other functional traits, including crop chemical profiles (Choi et al. 2014), which are also known to be important host identification cues for cruciferous pests (Nielsen 1988, Renwick and Radke 1988), and 3) color can be measured easily in the field and would be straightforward for farmers to manipulate. Finally, we evaluate the potential for varietal mixtures to serve as a profitable form of crop diversification by measuring their effect on labor costs and profitability. We predict that (i) the effect of varietal mixtures on pest incidence/abundance and crop damage will depend on landscape context and time of growing season (e.g. early versus late season), (ii) varietal color richness will mediate the effect of mixtures on pests, (iii) increasing intraspecific crop diversity will increase grower profits.

We investigated these predictions by measuring pest incidence and abundance, crop damage, and aspects of grower profitability in farmer fields located across a gradient of cropland cover in upstate New York during early and late season *B. oleracea* plantings.

Methods

STUDY SYSTEM

We sampled early and late season insect pests on crucifers in the Finger Lakes region of New York State on farms growing the following *B. oleracea* varieties: broccoli, brussels sprouts, cabbage, cauliflower, collards, kale, and kohlrabi. *Brassica oleracea* contains a large amount of intraspecific variation (Ahuja et al. 2011), which increased our likelihood of detecting an effect of varietal mixtures and made it easy to focus on a conspicuous crop trait, plant color, that could be mediating herbivore abundance. We focused on two important pests of crucifers in this region: the foliar feeding lepidopteran *P. rapae* and flea beetles (*Phyllotreta cruciferae* and *Phyllotreta striolata*) (Ahuja et al. 2011). In our study region, crucifers are planted multiple times from April through August and harvested from July through November (Seaman 2013). Flea beetles are dominant early in the season and their populations begin to decline in June, while *P. rapae* populations peak later in the season, typically after June (Seaman 2013). To address these seasonal differences, we focused our sampling on the late season planting in 2013 to capture *P. rapae* dynamics, and the early season planting in 2014 to capture flea beetle dynamics.

SURVEY DESIGN

We selected farms growing *B. oleracea* varieties in fields with low (one variety) to high (six varieties) numbers of varieties (i.e. varietal richness). We also recorded the number of varietal colors (color richness) in each field. It is important to note that varietal richness and color richness can vary independently from one another. For example, farmers may plant a purple sub-variety of cauliflower, a white sub-variety of cauliflower, and a green sub-variety of

broccoli in the same field. In this scenario, we would record two varieties (cauliflower and broccoli), but three colors (purple, white, and green).

We monitored pest incidence and abundance at 19 fields on 14 farms in the early season and 23 fields on nine farms in the late season, which included all farms from the early season survey. Farms were separated by a minimum of 3.5 km in the early season and 4 km in the late season. Separation between fields associated with the same farm ranged from 40 m to 4680 m in the early season (mean = 870.7 m, median = 119 m) and 29 m to 2000 m in the late season (mean = 285.4 m, median = 150 m). The fields ranged in size from 21 m² to 26,246 m². Although agricultural management varied by farm, all farms were characterized by organic practices; not all farms were certified organic, but all followed organic production practices and no synthetic inputs were used (Table S1). Given the observational nature of our study, planting schemes varied across farms, yet all varieties present in mixtures were planted closely to one another. In other words, different varieties were either planted together within a row or planted next to one another in alternating rows. We did not observe varieties arranged in large blocks or strips.

We used the proportion of cropland as our landscape composition metric, a land cover type influential for flea beetles (Andersen et al. 2005) and *P. rapae* (Benson et al. 2003). Cropland in this region included vegetables, fruits, legumes, cereals, and fallow fields. We selected fields to represent a gradient of landscape complexity, ranging from simple landscapes comprised mostly of cropland (71% cropland) to complex landscapes with little cropland (5% cropland). We define landscapes with little cropland as complex because non-agricultural land in our study region is dominated by natural areas, including deciduous, evergreen, and mixed forests, wetlands, and pastures composed of clover, wildflowers, and grasses. Percent cropland at three spatial scales (500, 1000, and 1500 m radius of each field) was calculated using the 2013 and 2014 Crop Data Layers (USDA National Agricultural Statistics Service Cropland Data Layer), respectively, and ArcGIS software (ESRI, ArcMap version 10.1).

PEST SAMPLING METHODS

We captured early season pest dynamics by visually counting adult flea beetles on 30 plants in each field three times from May to early July. At each sample event, we randomly selected six points in each field. At each point, we visually inspected five consecutive plants for adult flea beetles. Each plant was assessed for pest damage using a damage index ranging from zero (no damage) to five (severe damage) based on methods from Macharia et al. (2005) (Table S2). To account for seasonal changes in pest incidence/abundance and crop damage, we partitioned our sampling schedule into three sampling periods two weeks in length: mid-May, early June, and late June to early July. Due to differences in farmers' planting and harvesting schedules, fields were sampled during at least two of the sampling periods, but never more than once per sampling period.

We measured the incidence and abundance of *P. rapae* in the late season by counting the number of larvae on 30 plants in each field from July through early September following the same random sampling scheme used in the early season survey. Based on planting and harvesting schedules, we partitioned our sampling schedule into five sampling periods two weeks in length: early July, late July, early August, late August, and early September. All fields were sampled one to five times over the growing season, but never more than once per sampling period.

CROP BUDGETS

We developed crop budgets for ten of the 19 farm fields sampled in the 2014 early season survey using a net present value (NPV) approach to calculate the cost of inputs, revenue generated by yield, and profitability (methods based on Atallah & Gómez, 2013; McCarl, 1982; Wiswall, 2009). The crop budgets provide the basis of the economic comparison between low and high diversity fields. NPV analysis calculates the difference between the present value of cash inflows and the present value of cash outflows, which enabled us to analyze the profitability of increasing varietal and color richness. We defined profitability as the total revenue generated

by yield minus total expenses. In the crop budgets, we categorized expenses by the type of cost. We explicitly evaluated the effect of intraspecific crop diversity on labor because it is one of the most limiting inputs for growers (McCarl 1982, Bronars 2014). Therefore, we separated expenses into two categories: input costs (transplant, pest management, weed management, and fertility costs) and labor costs. When possible, financial information was gathered directly from farmers' records. Incomplete farm records were augmented with the average input and output prices used by the other farms in the study.

STATISTICAL METHODS

For all analyses, we developed hypothesis-based linear models in R Statistical Software 3.4.1 (R Core Team 2017) to test our predictions that both local- and landscape-scale diversity would impact pest incidence/abundance and crop damage. We used variance inflation factors (VIF) to ensure that the explanatory variables included in our models were not collinear (Zuur et al. 2009). Based on methods in Zuur et al. (2009), we used a VIF cut-off value of three to define collinear variables; all explanatory variables included in our models were below this cut-off value, indicating that none of our predictors were collinear.

Each of the models discussed below were fitted separately using the percent cropland variable calculated at each of three spatial scales—500, 1000, and 1500 m—and Akaike Information Criterion (AIC) values were used to determine the most predictive scale (Burnham and Anderson 2002). Because we focused on late season pest dynamics in 2013 and early season dynamics in 2014, we analyzed each year separately. To facilitate interpretation, all figures were plotted on the transformed scale, but labeled with untransformed values. We used Mantel tests to check for spatial autocorrelation of landscape composition at farm fields, as well as for spatial autocorrelation between the fields and response variables. Mantel tests indicate our data were not spatially autocorrelated either year (see Tables S3 & S4 in Supporting Information).

Pest dynamics

To analyze pest incidence and abundance we used generalized linear mixed effect models fitted with the *glmer* function in the lme4 package (Bates et al. 2015). Explanatory variables included varietal richness, color richness, percent cropland, and two-way interactions between percent cropland and the local-scale predictors—varietal richness and color richness. We used a nested random effects design of sampling point nested within sampling period nested within field. By including field as a random effect, we accounted for variation in field size, planting scheme, and management style.

To accommodate zero-inflated and overdispersed count data, we employed manual two-step hurdle models (Zuur et al. 2009). This amounted to two separate models: one for the binary “presence” or “absence” of a pest (incidence), and the second for the number of individuals present (abundance). In the first step, we modeled pest incidence using a binomial distribution (logit link) to govern the binary outcome of whether a pest existed on that plant. In the second step, we modeled pest abundance when present (i.e., the non-zero outcomes) with a Poisson distribution (log link). To check for overdispersion in the Poisson models, we used the *overdisp.glmer* function in the RVAideMemoire package (Hervé, 2017). If the model was overdispersed, an observation level random effect was added to correct for overdispersion (Harrison 2014). To ensure our data was well-modeled by the specified distributions as well as to check for violations of homoscedasticity and linearity, we used the DHARMA package (Hartig 2017) in R; no anomalies were found. The slopes of fitted lines were estimated and compared using the *lstrends* function in the lsmeans package (Lenth 2016).

Crop damage

To evaluate how crop damage was affected by varietal richness, color richness, percent cropland, and the two-way interactions between percent cropland and the local-scale predictors, we fit linear mixed effects models using the *lmer* function (lme4 package, Bates et al., 2015). We analyzed the relationship between crop damage and pest incidence/abundance using linear mixed

effects models. Again, our random effects included sampling point nested within period nested within field. The effects of fixed factors and interaction terms were evaluated using Type II Wald χ^2 tests with the *Anova* function in the car package (Fox and Weisberg 2011).

Crop budgets

In addition to exploring the effect of varietal mixtures on overall field profitability, we were interested in their relationship with production costs (i.e., labor and input costs) and revenue generation. Thus, the crop budget dataset included response variables of profitability, labor costs, input costs, and revenue generated from crop yield. Given that labor costs, input costs, and revenue were variables used to calculate profitability, it is likely these variables are not independent of one another. To avoid a Type I error, we used a Holm's Procedure for multiple test correction. Corrected and uncorrected p-values are reported in the supplementary materials; we used corrected p-values to interpret our results. We lacked sufficient sample size (n=10 fields) to investigate the impact of landscape predictors on the economic response variables. Therefore, we included only local-scale predictors (i.e., varietal and color richness). Due to the small sample size, fields in the crop budget dataset only had one to two varietal colors.

Results

PEST DYNAMICS

The effect of varietal and color richness on pest incidence and abundance varied across the landscape and by pest. We show results at the 1000 m and 500 m scales for the early season and late season surveys, respectively, because these were the most predictive scales for the dynamics of the focal pest (see Table S5 in Supporting Information). In the early season, we found a significant interaction between landscape complexity and varietal richness (p=0.007; Table S5). There was a positive association between flea beetle incidence and varietal richness in complex landscapes (p<0.05; Fig. 1); However, this trend was reversed in simple landscapes

($\geq 50\%$ cropland) ($p < 0.05$; Fig. 1). We found no effect of color richness on flea beetles. We also found a landscape-dependent effect of varietal richness on *P. rapae* incidence in the late season ($p < 0.004$, Table S5). That is, increased varietal richness had a significant negative effect on *P. rapae* incidence, but only in complex landscapes ($\leq 20\%$ cropland) ($p < 0.01$; Fig. 2;). Similarly, as color richness increased, *P. rapae* abundance significantly decreased, but only in complex landscapes ($p < 0.001$; Fig. 3; Table S5). Furthermore, as the proportion of cropland in the landscape increased, the abundance of *P. rapae* larvae significantly decreased, indicating that *P. rapae* was less abundant in simple landscapes ($p < 0.05$; Table S5). Our results indicate that flea beetles and *P. rapae* had unique responses to the interaction between intraspecific *B. oleracea* diversity and landscape composition.

CROP DAMAGE

Flea beetles had no effect on crop damage in the early season, but crop damage was significantly associated with *P. rapae* abundance in the late season ($p < 0.001$; Fig. 4). Varietal richness and color richness were not significantly correlated with crop damage in either the early or late season survey. However, throughout the growing season, crop damage decreased significantly as the percent of cropland in the surrounding landscape increased ($p < 0.05$; Figs. 5 and 6). This effect was significant at the 1000 m and 1500 m scale in the early season survey and at 500 m and 1000 m scale in the late season survey.

CROP BUDGETS

Fields with two varietal colors had significantly higher profits than fields with only one varietal color ($p < 0.05$; Figure 7; Table S6). Moreover, increasing the number of colors in a field was associated with a significant increase in revenue ($p < 0.01$; Table S6), and a marginally significant reduction in labor costs ($p = 0.066$; Table S6) and input costs ($p = 0.068$; Table S6). We found no significant effect of varietal richness on profitability, revenue, labor costs, or input costs.

Discussion

Our findings highlight the importance of accounting for spatial and temporal variation while evaluating the efficacy of local management practices, as the effect of varietal mixtures on pest populations varied across landscapes and growing season. The variability we detected may partially explain the previously documented mixed effects of varietal crop mixtures on insect pests (e.g., Altieri & Schmidt, 1987; Cantelo & Sanford, 1984; Power, 1988, 1991). Moreover, we found that intraspecific variation in crop color can significantly influence pest populations and profitability, suggesting a trait-based approach could maximize the value of the ecosystem services provided by varietal mixtures.

In the early season, the incidence of flea beetles decreased significantly in response to intraspecific crop diversity in simple landscapes. A recent study on Japanese beetles (*Popillia japonica*) revealed that beetles foraging across a suite of host plant species induce detoxification enzymes allowing them to cope with a greater diversity of plant chemical defenses (Adesanya et al. 2016); however, this detoxification process incurs a high energetic cost (Karban and Agrawal 2002). Varieties of *B. oleracea* are known to vary widely in their phytochemical profiles, including compounds important to plant defense against herbivores (Ahuja et al. 2011). Fields with high *B. oleracea* diversity may present a greater diversity of phytochemicals, thus requiring flea beetles to increase production of detoxification enzymes. Furthermore, some insect herbivores exhibit a similar detoxification response when exposed to pesticides (Schuler 2011), and landscapes dominated by agriculture have been shown to have higher background levels of pesticides compared to landscapes with a high proportion of semi-natural habitats (Meehan et al. 2011). Flea beetles foraging in fields with high *B. oleracea* diversity surrounded by agriculture may experience relatively high enzymatic costs. An inability to detoxify an array of phytochemicals as well as pesticides may partially explain the negative relationship between intraspecific *B. oleracea* diversity and flea beetle incidence in simple landscapes.

In complex landscapes, intraspecific *B. oleracea* diversity had a positive effect on flea beetle incidence. While this result contradicts findings from other studies in agricultural systems

showing a negative relationship between intraspecific crop diversity and herbivore abundance (Koricheva and Hayes 2018), it is in line with multiple studies in natural systems demonstrating a positive association between intraspecific plant diversity and herbivore abundance (Crutsinger et al. 2006, McArt and Thaler 2013). Fields with high intraspecific diversity may provide a greater diversity of dietary resources, as suggested by the balanced diet hypothesis (Tilman 1982, DeMott 1998). Therefore, in complex landscapes where herbivores may be less exposed to pesticides, it could be that the nutritional benefits associated with dietary diversity outweigh the enzymatic costs associated with increased plant phytochemical diversity. We did not explicitly explore the role of phytochemicals in our study, as our primary goal was to investigate a crop trait (plant color) that is simple to categorize and that farmers could easily manipulate. While crop chemical profiles can be correlated with plant color, they also vary by plant age and structure, as well as abiotic conditions (Choi et al. 2014). Therefore, it is unlikely that a straightforward relationship of one crop variety, one chemical profile exists. The strong relationship between color richness and herbivore abundance established in our study suggests that color is a useful and logistically feasible management strategy for farmers to implement. This finding should motivate future research exploring whether color itself drives the observed effect on herbivores or if there are underlying chemical profiles associated with color that contribute to the color effects observed in this study.

In contrast to early season pest dynamics, varietal richness reduced the incidence of *P. rapae* in complex landscapes, but had no effect in simple landscapes. A recent robust quantitative synthesis of the effect of landscape composition on insect pest species revealed substantial variation in pest species' responses to landscape variables (Karp et al. 2018). Our results support these findings, as we showed that flea beetles and *P. rapae* exhibit contrasting responses to landscape composition. In NY State, *P. rapae* is a host for several parasitoid species (Shelton et al. 2002), which have been shown to cause high levels of mortality in early instars of *P. rapae* (Herlihy et al. 2012a). Non-crop habitats such as forests and wetlands are important sources of refuge and alternative foods for natural enemies (Landis et al. 2000), and thus their

populations are often higher in complex landscapes (reviewed in Chaplin-Kramer et al., 2011). Research in natural systems has demonstrated that intraspecific plant diversity supports a higher abundance and diversity of parasitoids (Jones et al. 2011). The suppressive effect of intraspecific crop diversity that we observed in complex landscapes could be a result of enhanced biocontrol services. In our study, *P. rapae* was significantly less abundant in simple landscapes compared to complex landscapes. This finding appears to be in conflict with the resource concentration hypothesis, which would suggest that herbivore abundance should be highest in areas with concentrated food resources (Root 1973). It could be that higher background levels of pesticides—often associated with simplified landscapes (Meehan et al. 2011)—reduced the overall abundance of *P. rapae* in these areas. Indeed, previous work suggests that the effect of pesticides can outweigh effects of landscape composition on pest abundance (Veres et al. 2013). The low density of *P. rapae* that we observed in simple landscapes may have hindered detection of an effect of varietal mixtures in these landscapes.

Our results suggest that varietal color is one crop trait that has the potential to influence some pest species. Color richness elicited the same response from *P. rapae* as varietal richness; in complex landscapes, increased color richness reduced the abundance of *P. rapae* larvae. Since varietal and color richness vary independently from one another and are not collinear, these results demonstrate that *P. rapae* responded to intraspecific variation in crop color in addition to overall varietal richness. Previous studies have demonstrated that color is an important plant trait in moderating insect populations and *P. rapae* in particular is known to use foliage color as a landing cue (Tsuji & Coe 2014). In some instances, plant color is also correlated with plant defense compounds (Malenčić et al. 2012, Green et al. 2015). Therefore, it is possible that *P. rapae* responded to chemical as well visual cues associated with color richness. In contrast, flea beetles did not respond to color richness, indicating that other plant traits may play a more important role in mediating their population dynamics. *Brassica oleracea* varieties also differ widely in plant structure and chemistry (Ahuja et al. 2011), and previous research has demonstrated that an herbivore's response to structural and biochemical traits in *B. oleracea*

crops can be species-specific (Santolamazza-Carbone et al. 2013). Future studies are needed to further tease apart the varietal traits underlying the effect of mixtures on different insect species.

Although intraspecific crop diversity significantly influenced pest populations under certain scenarios, it had no effect on crop damage in either early or late season plantings. Rather, crop damage was negatively correlated with the percent of cropland in the landscape throughout the growing season, consistent with the negative relationship between *P. rapae* abundance and percent cropland in the late season. In our study, lower crop damage in simple landscapes may be a result of reduced pest pressure. Although our early season sampling occurred before *P. rapae* reached peak abundance, it is possible that the effect of landscape complexity on crop damage in the early season planting was also driven by *P. rapae*, as its abundance would have been increasing towards the end of our sampling period (Seaman 2013).

Although we did not find an effect of varietal mixtures on crop damage in this study, one limitation was the unbalanced design of the varietal mixtures we sampled. Because we conducted our research on working farms, the particular varieties that were included in the mixtures varied from field to field. Given an increasing appreciation for the importance of plant trait diversity in moderating ecosystem services (Wood et al. 2015), the potential for crop varietal mixtures to support pest control services could likely be increased by deliberately designing mixtures to include specific varietal traits.

Our economic analysis suggests that varietal mixtures warrant further attention due to their potential to support economic services. Despite a relatively small sample size, our results demonstrate that varietal mixtures can enhance profitability, as we found that increasing color richness significantly increased profit. The effect of color richness on profit appears to be mediated via its effect on revenue, and potentially on labor and input costs, as well; we found that increased color richness was associated with a significant increase in revenue generated from yield, and a marginally significant reduction in labor and input costs. We suggest that the effect of color richness on revenue could be a result of enhanced pest control services. In complex landscapes, the abundance of *P. rapae* was reduced in plots with high color richness,

and *P. rapae* was associated with crop damage. Therefore, increasing color richness may have increased marketable yield without increasing, and potentially even decreasing, the amount of labor and inputs a grower had to allocate to pest management via a reduction in *P. rapae* abundance and crop damage. The fact that our economic analysis reveals an effect of color richness, but not varietal richness, is further indication that intraspecific variation in specific crop traits, rather than simply varietal diversity, drives ecological and economic services.

While the conclusions drawn from the economic portion of our study could be tempered by our limited sample size, our findings suggest that varietal mixtures could serve as a profitable management strategy and should motivate further research into their ability to mitigate implementation constraints associated with other diversification strategies. The finding that intraspecific crop diversity did not increase labor costs is particularly encouraging, as labor is often the most difficult input for growers to procure, particularly in the current U.S. context where the lack of a stable agricultural workforce has had substantial impacts on the national economy (Duvall 2017). Indeed, the farmers included in the economic portion of this study allocated an average of 47% of their input costs to labor. Therefore, a diversification practice that does not entail a tradeoff between yield services and labor expenditures could be quite valuable for growers. This finding underscores the importance of explicitly measuring the value of services as well as production costs to determine overall profitability, arguably the most relevant metric for agricultural producers.

Future studies should also evaluate consumers' willingness to purchase new varieties, particularly varieties that differ in color because this appears to be a varietal trait that is important for insect pest control. Currently, many super-markets around the world only offer one or a few varieties of a given crop species (Lamers et al. 2016). Evaluating consumer preferences for varietal diversity would be useful, since increased demand for diversification could provide an additional incentive for growers to implement varietal mixtures. The widespread adoption of varietal mixtures would require the availability of a diverse seed supply as well as markets for these varieties. Finally, to maximize value to growers, we suggest that future research on the

design of varietal mixtures consider economically important varietal attributes related to ease of cultivation, labor demands, and market value in addition to traits related to environmental adaptability and productivity. Such information would support the thoughtful design of varietal mixtures that maximize both ecological and economic services for growers.

Acknowledgements

We sincerely thank the growers who made this work possible by welcoming us onto their farms. We also wish to acknowledge A. Iverson, E. Lombardi, R. Perez-Alvarez, J. Peters, K. Poveda, and J. Thaler for valuable feedback and comments. L. Snyder was supported by the National Science Foundation (NSF) through a Graduate Research Fellowship and the Food Systems and Poverty Reduction Integrative Graduate Education and Research Traineeship at Cornell University (#DGE-0903371). A. Power received support from Cornell University, USDA-NIFA AFRI Grant (#2013-67013-21235), and the Collaborative Crop Research Program of the McKnight Foundation.

REFERENCES

- Adesanya, A., N. Liu, and D. W. Held. 2016. Host suitability and diet mixing influence activities of detoxification enzymes in adult Japanese beetles. *Journal of Insect Physiology* 88:55–62.
- Ahuja, I., J. Rohloff, and A. M. Bones. 2011. Defence Mechanisms of Brassicaceae : Implications for Plant-Insect Interactions and Potential for Integrated 2:311–348.
- Altieri, M. A. 1999. The ecological role of biodiversity in agroecosystems. *Agriculture, Ecosystems & Environment* 74:19–31.
- Altieri, M. A., and L. L. Schmidt. 1987. Mixing broccoli cultivars reduces cabbage aphid numbers. *California Agriculture*:24–26.
- Andersen, C. L., R. Hazzard, and R. V. A. N. Driesche. 2005. Overwintering and Seasonal Patterns of Feeding and Reproduction in *Phyllotreta cruciferae* (Coleoptera : Chrysomelidae) in the Northeastern United States. *Environmental Entomology* 34:794–800.
- Andow, D. a. 1991. Vegetational diversity and arthropod population response. *Rev. Entomol* 36:561–6.
- Atallah, S. S., and M. I. Gómez. 2013. Eastern Broccoli Crop Budgets. Charles H. Dyson School of Applied Economics and Management, Cornell University.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67.
- Benson, J., R. G. Van Driesche, A. Pasquale, and J. Elkinton. 2003. Introduced braconid parasitoids and range reduction of a native butterfly in New England. *Biological Control* 28:197–213.
- Bianchi, F. J. J. A., C. J. H. Booij, and T. Tschardtke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings. Biological sciences / The Royal Society* 273:1715–1727.
- Bronars, S. 2014. No longer home grown: how labor shortages are increasing America’s reliance on imported fresh produce and hampering U.S. economic growth. Page (A. M. Zeitlin, Ed.).

- Burnham, K. P., and R. Anderson. 2002. *Model Selection and Multimodel Inference: A practical information-theoretic approach*. Springer-Verlag, New York.
- Cantelo, W. W., and L. L. Sanford. 1984. Insect Population Response to Mixed and Uniform Plantings of Resistant and Susceptible Plant Material. *Environmental Entomology* 13:1443–1445.
- Cartea, M. E., M. Francisco, M. Lema, P. Soengas, and P. Velasco. 2010. Resistance of Cabbage (*Brassica oleracea capitata* Group) Crops to *Mamestra brassicae*. *Journal of Economic Entomology* 103:1866–1874.
- Chaplin-Kramer, R., M. E. O'Rourke, E. J. Blitzer, and C. Kremen. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters* 14:922–932.
- Chaplin-Kramer, R., P. de Valpine, N. J. Mills, and C. Kremen. 2013. Detecting pest control services across spatial and temporal scales. *Agriculture, Ecosystems and Environment* 181:206–212.
- Choi, S., S. Park, Y. P. Lim, S. Kim, J. Park, and G. An. 2014. Metabolite Profiles of Glucosinolates in Cabbage Varieties (*Brassica oleracea* var. *capitata*) by Season, Color, and Tissue Position 55:237–238.
- Crawford, K. M., and J. A. Rudgers. 2013. Genetic diversity within a dominant plant outweighs plant species diversity in structuring an arthropod community. *Ecology* 94:1025–1035.
- Crutsinger, G. M., M. D. Collins, J. a Fordyce, Z. Gompert, C. C. Nice, and N. J. Sanders. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science (New York, N.Y.)* 313:966–8.
- DeMott, W. R. 1998. Utilization of a Cyanobacterium and a Phosphorus-Deficient Green Alga As Complementary Resources By Daphnids. *Ecology* 79:2463–2481.
- Duvall, V. 2017. Worker shortage threatens U.S. Ag Sustainability. <https://www.fb.org/viewpoints/worker-shortage-threatens-u.s.-ag-sustainability>.
- Fox, J., and S. Weisberg. 2011. *An R Companion to Applied Regression, Second Edition*.

Second. Thousand Oaks CA.

Gardiner, M. M., D. A. Landis, C. Gratton, C. D. DiFonzo, M. O'Neal, J. M. Chacon, M. T.

Wayo, N. P. Schmidt, E. E. Mueller, and G. E. Heimpel. 2009. Landscape Diversity Enhances Biological Control of an Introduced Crop Pest in the North-Central USA. *Ecological Applications* 19:143–154.

Gliessman, S. 1985. Multiple Cropping Systems: A Basis for Developing an Alternative Agriculture. Pages 69–86 *Innovative Technologies for Lesser Developed Countries*.

Green, J. P., R. Foster, L. Wilkins, D. Osorio, and S. E. Hartley. 2015. Leaf colour as a signal of chemical defence to insect herbivores in wild cabbage (*Brassica oleracea*). *PLoS ONE* 10:1–20.

Harrison, X. A. 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* 2.

Hartig, F. 2017. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.1.5.

Herlihy, A. M. V, R. G. Van Driesche, M. R. Abney, J. Brodeur, R. A. Casagrande, D. A. Delaney, T. E. Elkner, S. J. Fleischer, D. S. Gruner, J. P. Harmon, G. E. Heimpel, K. Hemady, T. P. Kuhar, A. M. Shelton, A. J. Seaman, M. Skinner, R. Weinzierl, K. V. Yeargan, and Z. Szendrei. 2012. Distribution of *Cotesia rubecula* (Hymenoptera : Braconidae) and Its Displacement of *Cotesia glomerata* in Eastern North America (HYMENOPTERA : BRACONIDAE) AND ITS DISPLACEMENT OF.

Herve, M. 2017. RVAideMemoire: Diverse Basic Statistical and Graphical Functions. R package version 0.9-66.

Jones, T. S., E. Allan, S. A. Härril, J. Krauss, C. B. Müller, and F. J. F. Van Veen. 2011. Effects of genetic diversity of grass on insect species diversity at higher trophic levels are not due to cascading diversity effects. *Oikos* 120:1031–1036.

Karban, R., and A. A. Agrawal. 2002. Herbivore Offense. *Annual Review of Ecology and Systematics* 33:641–664.

Karp, D. S., R. Chaplin-Kramer, T. D. Meehan, E. A. Martin, F. DeClerck, H. Grab, C. Gratton, L. Hunt, A. E. Larsen, A. Martínez-Salinas, M. E. O'Rourke, A. Rusch, K. Poveda, M. Jonsson, J. A. Rosenheim, N. A. Schellhorn, T. Tschardtke, S. D. Wratten, W. Zhang, A. L. Iverson, L. S. Adler, M. Albrecht, A. Alignier, G. M. Angelella, M. Zubair Anjum, J. Avelino, P. Batáry, J. M. Baveco, F. J. J. A. Bianchi, K. Birkhofer, E. W. Bohnenblust, R. Bommarco, M. J. Brewer, B. Caballero-López, Y. Carrière, L. G. Carvalheiro, L. Cayuela, M. Centrella, A. Četković, D. C. Henri, A. Chabert, A. C. Costamagna, A. De la Mora, J. de Kraker, N. Desneux, E. Diehl, T. Diekötter, C. F. Dormann, J. O. Eckberg, M. H. Entling, D. Fiedler, P. Franck, F. J. Frank van Veen, T. Frank, V. Gagic, M. P. D. Garratt, A. Getachew, D. J. Gonthier, P. B. Goodell, I. Graziosi, R. L. Groves, G. M. Gurr, Z. Hajian-Forooshani, G. E. Heimpel, J. D. Herrmann, A. S. Huseh, D. J. Inclán, A. J. Ingraio, P. Iv, K. Jacot, G. A. Johnson, L. Jones, M. Kaiser, J. M. Kaser, T. Keasar, T. N. Kim, M. Kishinevsky, D. A. Landis, B. Lavandero, C. Lavigne, A. Le Ralec, D. Lemessa, D. K. Letourneau, H. Liere, Y. Lu, Y. Lubin, T. Luttermoser, B. Maas, K. Mace, F. Madeira, V. Mader, A. M. Cortesero, L. Marini, E. Martinez, H. M. Martinson, P. Menozzi, M. G. E. Mitchell, T. Miyashita, G. A. R. Molina, M. A. Molina-Montenegro, M. E. O'Neal, I. Opatovsky, S. Ortiz-Martinez, M. Nash, Ö. Östman, A. Ouin, D. Pak, D. Paredes, S. Parsa, H. Parry, R. Perez-Alvarez, D. J. Perović, J. A. Peterson, S. Petit, S. M. Philpott, M. Plantegenest, M. Plečaš, T. Pluess, X. Pons, S. G. Potts, R. F. Pywell, D. W. Ragsdale, T. A. Rand, L. Raymond, B. Ricci, C. Sargent, J.-P. Sarthou, J. Saulais, J. Schäckermann, N. P. Schmidt, G. Schneider, C. Schüepp, F. S. Sivakoff, H. G. Smith, K. Stack Whitney, S. Stutz, Z. Szendrei, M. B. Takada, H. Taki, G. Tamburini, L. J. Thomson, Y. Tricault, N. Tsafack, M. Tschumi, M. Valantin-Morison, M. Van Trinh, W. van der Werf, K. T. Vierling, B. P. Werling, J. B. Wickens, V. J. Wickens, B. A. Woodcock, K. Wyckhuys, H. Xiao, M. Yasuda, A. Yoshioka, and Y. Zou. 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences* 115:E7863–E7870.

- Koricheva, J., and D. Hayes. 2018. The relative importance of plant intraspecific diversity in structuring arthropod communities: a meta-analysis. *Functional Ecology*:1–14.
- Lamers, H. A. H., F. Kruijssen, B. Sthapit, and R. Rao. 2016. How can markets contribute to conservation of agricultural biodiversity on farms; from theory into practise. Pages 263–284 *in* B. R. Sthapit, H. A. H. Lamers, R. Rao, and A. Bailey, editors. *Tropical Fruit Tree Diversity: Good Practices for In situ and On-farm Conservation*. Routledge, Abingdon.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annals of the ...* 45:175–201.
- Lenth, R. V. 2016. Least-Squares Means: The R Package lsmeans. *Journal of Statistical Software* 69:1–33.
- Letourneau, D. K., I. Armbrrecht, B. S. Rivera, J. M. Lerma, E. J. Carmona, M. C. Daza, S. Escobar, V. Galindo, C. Gutiérrez, S. D. López, J. L. Mejía, A. M. A. Rangel, J. H. Rangel, L. Rivera, C. A. Saavedra, A. M. Torres, and A. R. Trujillo. 2011. Does plant diversity benefit agroecosystems? A synthetic review. *Ecological applications* : a publication of the Ecological Society of America 21:9–21.
- Macharia, I., B. Lo, and H. De Groot. 2005. Assessing the potential impact of biological control of *Plutella xylostella* (diamondback moth) in cabbage production in Kenya. *Crop Protection* 24:981–989.
- Malenčić, D., J. Cvejić, and J. Miladinović. 2012. Polyphenol Content and Antioxidant Properties of Colored Soybean Seeds from Central Europe. *Journal of Medicinal Food* 15:89–95.
- McArt, S. H., and J. S. Thaler. 2013. Plant genotypic diversity reduces the rate of consumer resource utilization. *Proceedings. Biological sciences / The Royal Society* 280:20130639.
- McCarl, B. A. 1982. Cropping Activities in Agricultural Sector Models : A Methodological Proposal. *American Journal of Agricultural Economics* 64:768–772.
- Meehan, T. D., B. P. Werling, D. A. Landis, and C. Gratton. 2011. Agricultural landscape simplification and insecticide use in the Midwestern United States. *Proceedings of the*

- National Academy of Sciences 108:11500–11505.
- Nielsen, J. K. 1988. Crucifer-feeding Chrysomelidae: Mechanisms of host plant finding and acceptance. Page *in* P. Jolivet, E. Petipierre, and T. H. Hsiao, editors. *Biology of Chrysomelidae*. Dordrecht.
- Power, A. G. 1988. Leafhopper response to genetically diverse maize stands. *Entomologia Experimentalis et Applicata* 49:213–219.
- Power, A. G. 1991. Virus Spread and Vector Dynamics in Genetically Diverse Plant Populations
Author (s): Alison G . Power Reviewed work (s): Published by : Ecological Society of America Stable URL : <http://www.jstor.org/stable/1938917> . VIRUS SPREAD AND VECTOR DYNAMICS. *Entomologia Experimentalis et Applicata* 72:232–241.
- Power, A. G. 2010. Ecosystem services and agriculture: tradeoffs and synergies. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 365:2959–2971.
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Renwick, J. A. A., and C. . Radke. 1988. Sensory cues in host selection of oviposition by the cabbage butterfly, *Pieris rapae*. *Journal of Insect Ecology* 34:251–257.
- Root, R. B. 1973. Organization of a Plant-Arthropod Association in Simple and Diverse Habitats : The Fauna of Collards (*Brassica Oleracea*). *Ecological Monographs* 43:95–124.
- Santolamazza-Carbone, S., P. Velasco, J. Selfa, P. Soengas, and M. E. Cartea. 2013. Intraspecific variation of host plant and locality influence the Lepidopteran-parasitoid system of *Brassica oleracea* crops. *Journal of Economic Entomology* 106:1134–1144.
- Schuler, M. A. 2011. P450s in plant-insect interactions. *Biochimica et Biophysica Acta* 1814:36–45.
- Seaman, A. 2013. 2013 Organic Cole Crops Production Guide for. Ithaca.
- Shelton, A. M., W. T. Wilsey, E. R. Hoebeke, and M. A. Schmaedick. 2002. Parasitoids of cabbage lepidopteran in central New York. *Journal of Entomological Science* 37:270–271.
- Sinkkonen, A., E. Somerkoski, U. Paaso, J. K. Holopainen, M. Rousi, and J. Mikola. 2012.

- Genotypic variation in yellow autumn leaf colours explains aphid load in silver birch. *New Phytologist* 195:461–469.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ.
- Tooker, J. F., and S. D. Frank. 2012. Genotypically diverse cultivar mixtures for insect pest management and increased crop yields.
- Tscharntke, T., R. Bommarco, Y. Clough, T. O. Crist, D. Kleijn, T. A. Rand, J. M. Tylianakis, S. van Nouhuys, and S. Vidal. 2007. Conservation biological control and enemy diversity on a landscape scale. *Biological Control* 43:294–309.
- Tscharntke, T., J. M. Tylianakis, T. a. Rand, R. K. Didham, L. Fahrig, P. Batáry, J. Bengtsson, Y. Clough, T. O. Crist, C. F. Dormann, R. M. Ewers, J. Fründ, R. D. Holt, A. Holzschuh, A. M. Klein, D. Kleijn, C. Kremen, D. a. Landis, W. Laurance, D. Lindenmayer, C. Scherber, N. Sodhi, I. Steffan-Dewenter, C. Thies, W. H. van der Putten, and C. Westphal. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews* 87:661–685.
- Tsuji, J., and L. Coe. 2014. Effects of Foliage Color on the Landing Response of *Pieris rapae* (Lepidoptera: Pieridae). *Environmental Entomology* 43:989–994.
- Veres, A., S. Petit, C. Conord, and C. Lavigne. 2013. Does landscape composition affect pest abundance and their control by natural enemies? A review. *Agriculture, Ecosystems and Environment* 166:110–117.
- Wiswall, R. 2009. The organic farmer's business handbook. Page (B. Watson and L. Jorstad, Eds.). Chelsea Green Publishing, White River Junction.
- Wood, S. A., D. S. Karp, F. DeClerck, C. Kremen, S. Naeem, and C. A. Palm. 2015. Functional traits in agriculture: Agrobiodiversity and ecosystem services. *Trends in Ecology and Evolution* 30:531–539.
- Yang, E.-C., D.-W. Lee, and W.-Y. Wu. 2003. Action spectra of phototactic responses of the flea beetle, *Phyllotreta striolata*. *Physiological Entomology* 28.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Pages 1–574 in M. Gail, K. Krickeberg, J. Samet, A. Tsiastis, and W. Wong, editors. *Mixed effects models and extensions in ecology with R*. Springer, New York.

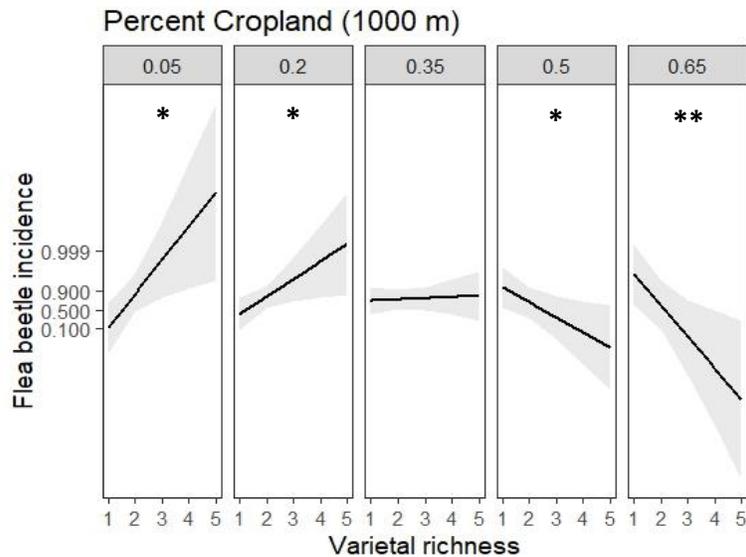


Fig. 2.1. Model estimates with 95% confidence intervals for the relationship between flea beetle incidence and varietal richness across a gradient of landscape complexity (5, 20, 35, 50, and 65 % cropland 1000 m) in the early season planting. We show percent crop land at equal intervals that portray the range of landscape complexity in our study region and are well represented in our dataset. Slope significantly different from zero: * $p < 0.05$, ** $p < 0.01$.

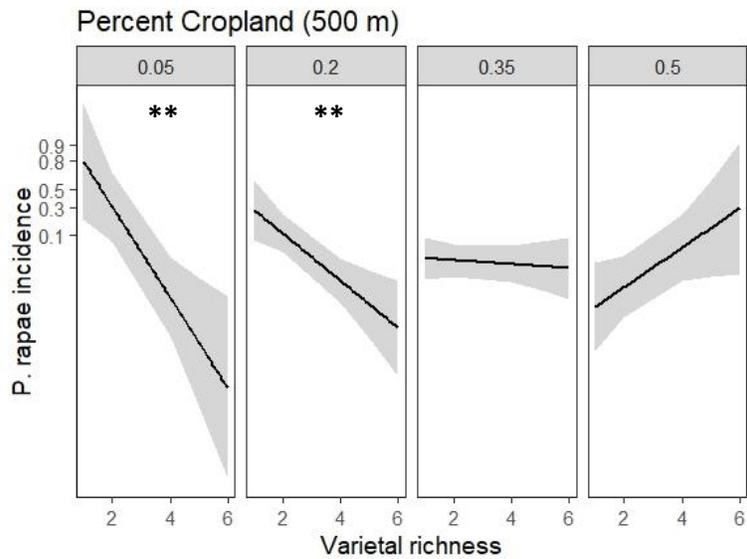


Fig. 2.2. Modelled effect of varietal richness on *P. rapae* incidence across a gradient of landscape complexity (5, 20, 35, and 50 % cropland 500 m) in the late season planting. We show percent crop land at equal intervals that portray the range of landscape complexity in our study region and are well represented in our dataset. Figure shows regression slopes with 95% confidence intervals. Slope significantly different from zero: ** $p < 0.01$.

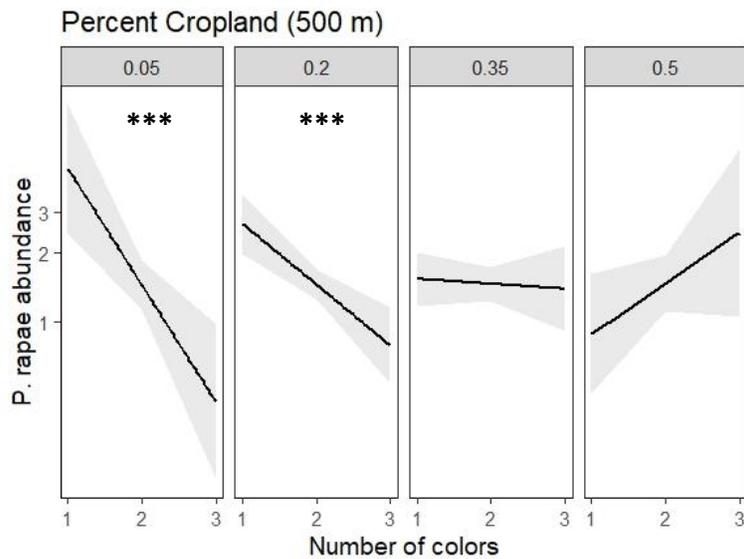


Fig. 2.3. Modelled effect of the number of colors in a field on *P. rapae* abundance across a gradient of landscape complexity (5, 20, 35, and 50 % cropland 500 m) in the early season planting. We show percent crop land at equal intervals that portray the range of landscape complexity in our study region and are well represented in our dataset. Figure shows regression slopes with 95% confidence intervals. Slope significantly different from zero: *** $p < 0.001$.

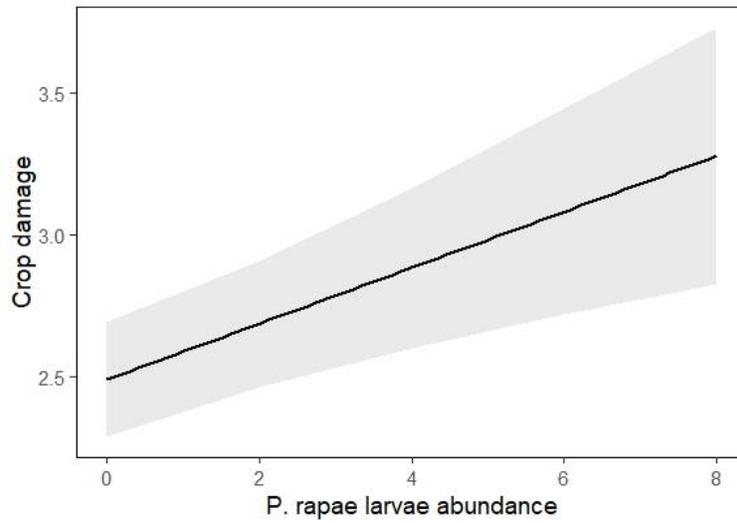


Fig. 2.4. Model estimates with 95% confidence intervals for the relationship between crop damage and *Pieris rapae* larvae abundance (predicted mean number of *P. rapae* larvae per plant) in the late season planting.

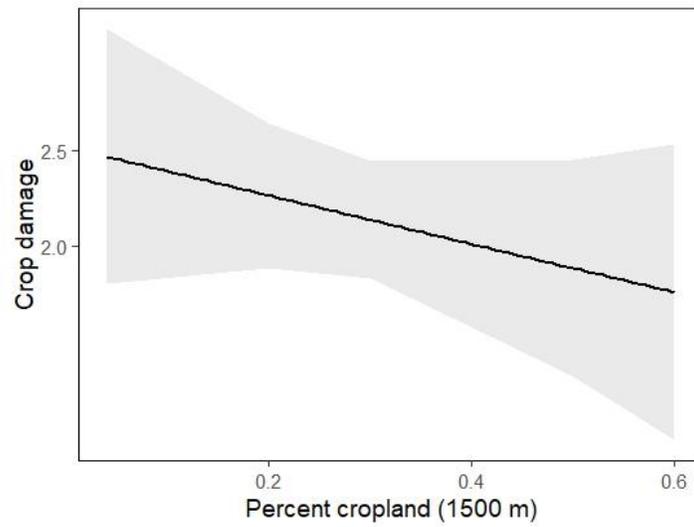


Fig. 2.5. Model estimates with 95% confidence intervals for the relationship between crop damage and percent cropland at the 1500 m scale in the early season planting.

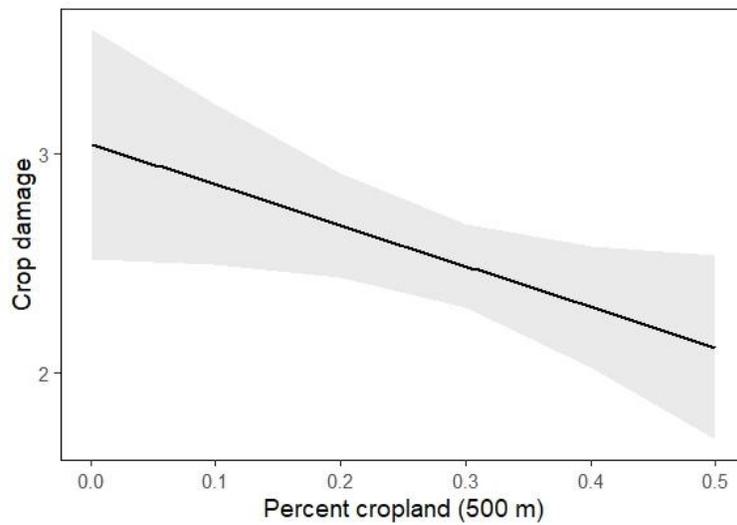


Fig. 2.6. Model estimates with 95% confidence intervals for the relationship between crop damage and percent cropland at the 500 m scale in the late season planting.

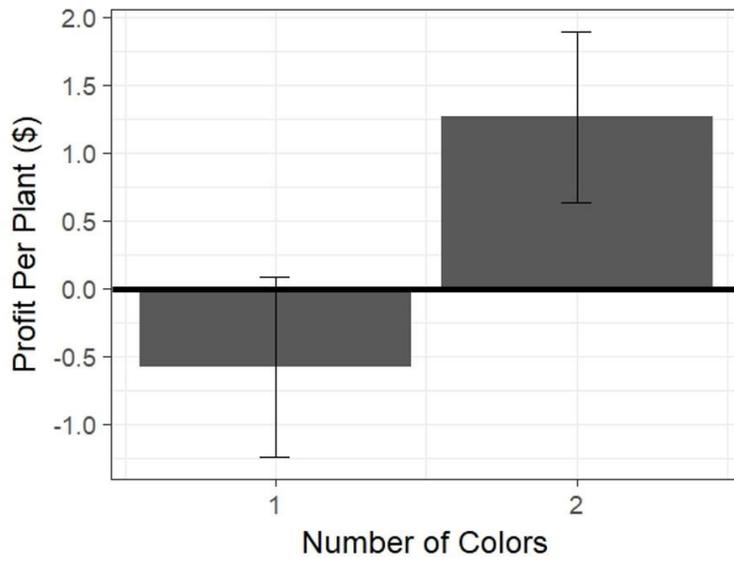


Fig. 2.7. Effect of color richness on profitability (model mean estimate \pm SE). Profitability was calculated using a net present value analysis. We defined profitability as the total revenue generated by yield minus total expenses.

CHAPTER THREE
VARIETAL IDENTITY, NOT VARIETAL RICHNESS, PREDICTS PEST ABUNDANCE
AND CROP DAMAGE

Abstract

1. A growing body of research demonstrates that enhancing intraspecific crop diversity in the form of varietal mixtures can support multiple ecosystem services, including crop productivity and pest suppression. However, most research on varietal mixtures has focused on whether intraspecific crop diversity benefits exist and there has been less emphasis on identifying the mechanisms driving these effects. Hypotheses developed for species-level effects on ecosystem processes could provide a useful framework for varietal mixtures and suggest biodiversity effects can be driven by two main mechanisms, diversity per se or the presence of a particular species (i.e., identity effects).
2. We applied this framework to varietal mixtures of *Brassica oleracea* to test whether varietal richness (i.e., diversity) or varietal identity mediated the abundance of two cruciferous pests (*Pieris rapae* and *Plutella xylostella*), crop damage, and yield. Using two separate common garden experiments, we leveraged the broad trait variation present in *B. oleracea* crops to test our questions across two crop traits, plant morphology and color, which are known to influence the behavior of cruciferous pests.
3. Across both experiments, varietal identity, rather than varietal richness, mediated pest abundance and crop damage. Despite significant effects of mixtures on crop damage, we found no significant effect of mixtures on crop yield in either experiment. Interestingly, *P. xylostella* responded to intraspecific crop variation in both the morphology and color experiment, whereas intraspecific crop diversity only influenced *P. rapae* in the morphology experiment. In some instances, monocultures offered stronger pest control services than mixtures, but in other scenarios varietal mixtures received significantly less crop damage compared to monocultures.

These findings suggest that while monocultures may be superior to mixtures in some cases, planting a monoculture of the wrong variety can exacerbate pest problems.

4. *Synthesis and applications.* Taken together, our results underscore the importance of identifying and maintaining the right kind of diversity. The strong identity effects we observed suggest that, for pest control services, management strategies that target influential crop varieties will be more effective than those that focus on maximizing varietal diversity more broadly. To strengthen pest control services in varietal mixtures, we recommend additional research to tease apart the role of functional trait diversity in varietal mixtures on different pest species.

INTRODUCTION

Increasing agricultural diversity has been shown to provide ecosystem services that support agricultural production (Power 2010, Letourneau et al. 2011, Iverson et al. 2014). Enhancing intraspecific crop diversity—genetic diversity within one species—through the use of varietal mixtures is one form of crop diversification that is receiving increasing attention for its potential to support pest control and yield services (Tooker and Frank 2012, Reiss and Drinkwater 2018). In fact, studies in natural systems indicate that intraspecific plant diversity can play as important a role as plant species diversity in regulating important ecosystem processes, such as structuring arthropod herbivore communities and supporting plant productivity (Crutsinger et al. 2006, Jones et al. 2011, Cook-Patton et al. 2011, Crawford and Rudgers 2013), and these services are particularly relevant to crop production. Moreover, varietal mixtures have the potential to provide growers with a logistically feasible diversification strategy, as they require relatively minor changes to existing simplified agricultural systems (Tooker & Frank 2012). For instance, varieties of the same crop species often have similar growing requirements and may be marketed similarly, meaning farmers could leverage their existing agronomic knowledge and expand varietal diversity in a crop species they currently grow (Wilhoit 1992, Tooker and Frank 2012).

Implementation of varietal mixtures to support pest control and yield services in agricultural systems shows promise (reviewed in Tooker & Frank, 2012), yet much remains to be explored. While there is a strong body of evidence demonstrating the beneficial effect of varietal mixtures on crop production and yield stability (Reiss and Drinkwater 2018), fewer studies have explored the effect of varietal mixtures on arthropod pests and crop damage in agricultural systems (Tooker and Frank 2012, Koricheva and Hayes 2018). A recent meta-analysis demonstrated that crop mixtures were associated with a significant reduction in arthropod pest abundance, but the same study found no effect of mixtures on crop damage (Koricheva and Hayes 2018). However, these non-significant outcomes were based on the results of a small number of studies (n=6), indicating further research is needed before broader conclusions can be drawn. Moreover, the effect of varietal mixtures has been shown to vary depending on the pest species in question (Cantelo and Sanford 1984, Power 1988, Abdala-Roberts et al. 2015). For example, Abdala-Roberts et al. (2015) found varietal mixtures of *Capsicum chinense* peppers reduced attacks by leafminer larvae, but had no effect on fruit-eating weevils. Thus, to more fully understand how varietal mixtures influence pest communities, we need additional empirical studies that simultaneously consider multiple pest species, as well as further research into the potential for varietal mixtures to mediate crop damage.

Most research on varietal mixtures in agricultural systems has focused on whether or not intraspecific crop diversity benefits exist; identifying the mechanisms underlying the effect of varietal mixtures on pest abundance and crop production has received less attention (Hughes et al. 2008, Moreira et al. 2016). Hypotheses developed for species-level effects on ecosystem processes, such as plant productivity, could provide a useful framework for varietal mixtures. This body of work suggests that biodiversity effects may be driven by various mechanisms, which are either related to diversity per se (e.g., species richness) or the presence of a particular species (e.g., species identity). For instance, plant species diversity can enhance productivity through complementarity in resource use when species utilize resources in different ways, or through facilitation when one species enhances the resource use of another species (Loreau et al.,

2001; Loreau & Hector, 2001; Tilman et al., 1997). In a study examining the effect of plant diversity on productivity in perennial cropping systems, polycultures consistently outperformed component monocultures due to complementarity among species (Picasso et al. 2011). Similarly, the resource concentration hypothesis predicts plant species diversity can reduce insect pest populations by making it harder for pests to locate suitable host plants (Tahvanainen and Root 1972). Increasing the diversity of plant traits is one explanation for this effect. For example, in corn-bean-squash systems that exhibit high variation in plant morphology, beetle pests were significantly less abundant in polycultures than in monocultures, potentially due to unfavorable microclimates and reduced mobility resulting from increased plant morphological diversity (Risch 1981). In other instances, the presence of a particular plant species (e.g., species identity), rather than diversity, drives ecosystem functions. For example, in grassland ecosystems, the presence of nitrogen-fixing legume species was more predictive of plant productivity than species diversity (Tilman and Knops 1997). Plant species identity can also significantly influence the presence of particular insect pest species (Parry et al. 2015).

In this study, we apply the framework derived from species-level research to assess whether varietal richness or varietal identity play a more important role in mediating agroecosystem functions in varietal mixtures. Specifically, we test two hypotheses: 1) varietal richness (i.e., diversity) drives the effect of mixtures on pest abundance and crop production, and 2) varietal identity drives the effect of mixtures on pest abundance and crop production. *Brassica oleracea* is an ideal study system in which to address these questions as it encompasses a broad range of intraspecific trait variation, increasing our likelihood of detecting an effect of varietal mixtures. We take advantage of this trait variation to test our hypotheses across two different crop traits, plant morphology and color, which are known to influence landing and oviposition preference of cruciferous lepidopterans (Jankowska 2006, Tsuji and Coe 2014). *Brassica oleracea* crops are attacked by multiple pests, which also allows us to assess whether herbivore response to varietal mixtures is consistent across pest species. Specifically, we evaluate how mixtures of *B. oleracea* varieties that vary in morphology and color affect the abundance of two

cruciferous pest species common throughout North America—*Pieris rapae* and *Plutella xylostella* (Capinera 2014, Philips et al. 2014). In addition, we explore the effects of varietal mixtures on the quality and quantity of crop production by measuring crop damage and yield, as these are the services of ultimate importance to farmers. By identifying whether varietal richness or identity drive these effects, we aim to provide guidance on whether agricultural practitioners should maximize richness by growing as many varieties as possible or focus their efforts on increasing the abundance of a few key varieties that support pest suppression and crop production.

MATERIALS AND METHODS

COMMON GARDEN EXPERIMENTS

We conducted two common garden experiments at the Homer C. Thompson Research Farm at Cornell University in Ithaca, NY from early June through early September 2016. The goal of the experiments was to examine the relative effect of varietal richness versus varietal identity across two plant traits, morphology and color.

In the first experiment, we studied the effect of intraspecific variation in crop morphology using three varieties of *B. oleracea*: broccoli (var. *italica* cv. Bay Meadows), cabbage (var. *capitata* cv. Gonzales), and kale (var. *acephala* cv. Starbor). The harvestable portions of these varieties represent three different plant morphologies; the edible portions of broccoli are the flower stalk and immature flowers, while in kale and cabbage the harvestable portions are the leaves, which either grow separately or tightly clumped as a head. We manipulated varietal richness by growing broccoli, cabbage, and kale in all combinations from monocultures to three variety mixtures. In total, we had seven treatments: broccoli monoculture, kale monoculture, cabbage monoculture, kale-broccoli mixture, kale-cabbage mixture, broccoli-cabbage mixture, and broccoli-cabbage-kale mixture. As each variety represented a different plant morphology, we were able to test for an effect of varietal richness (i.e., one, two, or three variety mixtures), as well as test for identity effects by assessing whether the performance of particular combinations

of varieties (i.e., varietal composition) or the presence of a particular variety affected pest abundance, crop damage, and yield. To reduce variation in other crop traits such as plant chemistry, which can co-vary with color (Malenčić et al. 2012, Green et al. 2015), all three varieties used in the morphology experiment were green .

We applied the same experimental design to the color common garden experiment using three varieties of cauliflower (var. botrytis): Graffiti (purple), Vitaverde (green), and Denali (white). We varied varietal richness by growing the three varieties of cauliflower in one, two, and three color mixtures. Our seven color treatments included: purple monoculture, green monoculture, white monoculture, purple-green mixture, purple-white mixture, green-white mixture, and purple-white-green mixture. Similar to the morphological experiment, our goal was to test for an effect of varietal richness (i.e., one, two, or three variety mixtures), as well as explore the role of identity effects by assessing whether varietal composition or the presence of a particular variety affected pest abundance, crop damage, and yield. The cauliflower varieties differed in color, but had the same leaf and head morphology, enabling us to independently test for effects of intraspecific color variation.

In both experiments, treatments were replicated in 6 randomized blocks. All plots measured 4 x 4 m and contained 60 plants arrayed in 6 rows with 10 plants per row, for a total of 2,520 plants per experiment. Plants were transplanted 45 cm apart with 76 cm between rows. Each row was planted with a single variety; when multiple varieties were present in a plot, varieties were planted in alternating rows. Within an experiment, plots were separated by 3 m and blocks by 6 m. The two experiments were separated by 12 m of bare ground.

All seeds were procured from Johnny's Seeds and grown in a Cornell greenhouse using Lambert planting media. While in the greenhouse, plants were fertilized weekly. After eight weeks in the greenhouse, plants were moved outdoors to harden for one week. All plants were nine weeks old at the time they were transplanted into the field in early June 2016. Prior to planting, a pre-emergent herbicide was applied to the field to reduce the effect of other naturally occurring plant species, and fertilizer and herbicide was applied according to current

recommendations (Ristow et al. 2007). During the experiment, plots were weeded by hand and mechanical cultivation was used between plots to reduce weed pressure as needed.

Plants were left in the field to establish for two weeks before arthropod sampling began. The morphology experiment was sampled every other week between early July through early August (three sample events) and the color experiment every other week between late June through late July (three sample events). During each sample event, the inner 24 plants of each plot were visually inspected for *P. rapae* and *P. xylostella*. For *P. rapae*, we counted the number of eggs, larvae, and pupae on each plant. However, we excluded *P. rapae* pupae from our analysis as they occurred in extremely low numbers (morphology experiment $n=21$, color experiment $n=7$). For *P. xylostella*, we counted the number of larvae and pupae, but not eggs, as their small size (less than 0.5 mm in length) makes it difficult to accurately measure their abundance in the field. During visual inspections for arthropods, we also assessed pest damage on the inner 24 plants of each plot using a crop damage scoring metric that was standardized across all varieties. Plants were scored for damage on an ordinal scale from zero (no damage) to five (high damage) based on methods from Macharia, Lo, & Groote (2005) (Table 1). Once plants reached maturity, we harvested the inner 24 plants of each plot to assess yield by weighing the harvestable portion of each variety. To compare yield across treatments containing different varieties, we normalized the yield data by computing Z scores.

STATISTICAL ANALYSIS

We analyzed the two common garden experiments separately, but used identical statistical analyses for both, as outlined below. We used hypothesis-based models in R Statistical Software 3.4.4 (R Core Team 2017) to determine whether varietal richness or varietal identity affected arthropod pest abundance, crop damage, and yield. For all analyses, we examined plot-level data and used restricted maximum likelihood (REML) to estimate variance parameters in linear mixed models (lme4 package, Bates, Maechler, Bolker, & Walker, 2015).

For each experiment, we partitioned our analysis into two stages. In the first stage, our objective was to determine whether the level of varietal richness in a plot (one, two, or three varieties), regardless of varietal composition, affected pest abundance, crop damage, and yield. In the second stage of our analysis, we tested for an identity effect by determining whether varietal composition and/or the presence of particular varieties influenced arthropod pest abundance, crop damage, and yield. In both stages of analysis, our response variables included the abundance of *P. rapae* larvae and eggs, *P. xylostella* larvae and pupae, and crop damage and harvestable yield. We log-transformed the abundance of arthropods to improve normality and homogeneity of variance.

Varietal Richness

To address our first objective, we included varietal richness (three levels) as a fixed effect. For pest abundance and crop damage, our random effects included spatial block crossed with sample event. We used only spatial block as a random effect when analyzing yield, as plants were harvested once. Results are reported as Type III sum of squares. We also tested for significant differences between the three levels of varietal richness by estimating and comparing least-squares means using Tukey's multiple comparison procedure with the *lsmeans* function in the *lsmeans* package (Lenth 2016).

Identity Effects

In the second stage of our analysis, we created linear mixed models with treatment as a fixed effect (seven levels for each experiment) to evaluate the effect of varietal composition on our response variables. As in the first stage of our analysis, we included spatial block crossed with sample event as random effects when analyzing pest abundance and crop damage, and spatial block as a random effect when analyzing yield. The effect of treatment is reported as a Type III sum of squares. To test for significant differences between treatments, we estimated and compared least-squares means using the *lsmeans* function in the *lsmeans* package with a Tukey's

adjustment for multiple comparisons (Lenth 2016). To evaluate whether identity effects were at play, we compared the magnitude of response variables in one-variety treatments with their magnitude in two-variety and three-variety mixtures. If differences between multi-variety mixtures and monocultures of their components were not significant, an identity effect was implicated (Long and Finke 2014). To tease apart which varieties were responsible for any identity effects, we conducted preplanned contrasts to assess how treatments containing a particular variety influenced our response variables compared to treatments without that particular variety. If the magnitude of response variables was significantly different between plots with and without a particular variety, we would infer that particular variety was contributing to an identity effect (Long and Finke 2014).

RESULTS

To differentiate between the morphology and color experiments in our results, we will refer to varietal richness as either morphological richness or color richness and to varietal composition as either morphological composition or color composition.

EFFECTS OF INTRASPECIFIC MORPHOLOGICAL VARIATION

We found no significant effect of morphological richness on pest abundance, crop damage, or yield (Table S1). However, we found a significant effect of morphological composition on the abundance of *P. rapae* eggs ($p < 0.001$; Fig. 1a; Table S2) and larvae ($p < 0.001$; Fig. 1b; Table S2), and *P. xylostella* larvae ($p < 0.01$; Fig. 1c; Table S2). In other words, the abundance of these pests varied significantly across the seven trait combinations. There was no effect on *P. xylostella* pupae ($p = 0.09$; Table S2).

Overall, the abundance of *P. rapae* eggs and larvae, and *P. xylostella* larvae varied significantly across single-trait plots (Fig. 1). Interestingly, the abundance of *P. rapae* eggs and larvae, and *P. xylostella* larvae was consistently higher in monocultures of broccoli than in monocultures of kale (Fig. 1). Furthermore, mixtures with two and three traits did not

consistently perform differently from their single trait components (Fig. 1). Taken together, these results suggest identity effects contributed to the observed differences across treatments. In particular, the three-trait treatment consistently had similar numbers of *P. rapae* eggs and larvae, and *P. xylostella* larvae as monocultures of broccoli (Fig. 1), suggesting broccoli in particular may have contributed to an identity effect.

When we compared pest abundance in mixtures that lacked a particular variety to those where the variety was present, we found further evidence of identity effects. In particular, we found a significantly lower abundance of *P. rapae* eggs ($t = -3.34$; $p < 0.01$) and larvae ($t = -2.2$; $p < 0.05$), and *P. xylostella* larvae ($t = -3.27$; $p < 0.01$) in plots with kale compared to plots without kale (Fig. 2a). In contrast, plots with broccoli had significantly more *P. rapae* eggs ($t = 9.37$; $p < 0.001$) and larvae ($t = 5.33$; $p < 0.001$), and *P. xylostella* larvae ($t = 2.62$; $p < 0.05$) than plots without broccoli (Fig. 2b). These results provide support for a dominant role of kale and broccoli in the varietal mixtures. We found no significant differences between plots with and without cabbage.

The level of crop damage also varied significantly across the seven morphology treatments ($p < 0.001$; Fig. 3; Table S2). As with pest abundance, the level of crop damage varied across single-trait plots, but there were no consistent differences in crop damage between multi-trait mixtures and their components (Fig. 3). As with pest abundance, the largest difference in crop damage was between monocultures of kale and monocultures of broccoli (Fig. 3). Therefore, identity effects also appear to drive the effect of mixtures on crop damage. Comparing crop damage in plots with and without particular varieties provided further evidence for the role of varietal identity in mixtures, with kale emerging again as a dominant variety. Plots with kale received significantly less crop damage than plots without kale ($t = -4.43$, $p < 0.001$; Fig. 4). Although plots with broccoli had significantly higher pest abundance than plots without broccoli, the presence of broccoli had no significant effect on crop damage. Despite the significant effect of morphological composition and identity on crop damage, we found no effect on yield (Table S2).

EFFECTS OF INTRASPECIFIC COLOR VARIATION

Consistent with results from the morphology common garden experiment, we found no effect of color richness on our response variables (Table S3). However, in contrast to the effects of morphological composition on pest abundance, only *P. xylostella* larvae responded to color composition ($p < 0.01$; Fig. 5; Table S4). We detected no effect of color composition on *P. rapae* larvae or eggs, or on *P. xylostella* pupae (Table S4). We found significant differences in the average abundance of *P. xylostella* larvae across single-trait plots, with the largest difference arising between monocultures of Denali (white) and monocultures of Vitaverde (green) (Fig. 5). There was also no consistent difference in the abundance of *P. xylostella* larvae between multi-trait mixtures and their components (Fig. 5), which implicates an identity effect. When we compared *P. xylostella* larvae abundance in plots with a particular variety to plots without that variety, we found significantly more larvae in plots with Vitaverde than in plots without Vitaverde ($t = 2.16$, $p < 0.05$), providing further evidence of an identity effect (Fig. 6). We found no dominant effects of Graffiti (purple) or Denali varieties on pest abundance (Fig. 6).

As in the morphology experiment, we found a significant effect of color composition on crop damage ($p < 0.001$; Fig. 7; Table S4), but not on yield (Table S4). Again, identity effects appear to contribute to the effect of color composition on crop damage, as we found significantly higher levels of damage in plots with Vitaverde than in plots without Vitaverde ($t = 2.16$, $p < 0.05$), and significantly lower levels of damage in plots with Denali than in plots without ($t = -2.02$, $p < 0.05$) (Fig. 8). We found no significant differences in crop damage between plots with and without Graffiti ($t = -1.54$; $p = 0.13$; Fig. 8).

DISCUSSION

Varietal mixtures are increasingly recognized for their ability to enhance crop production in agroecosystems (Reiss and Drinkwater 2018), and show promise for supporting pest suppression services (Tooker and Frank 2012, Koricheva and Hayes 2018). Hypotheses developed from species-level research suggest these effects could be driven by diversity per se

(varietal richness) or by the presence of a particular variety (varietal identity) (Loreau et al., 2001). Depending on the mechanism at play, in some instances the most effective management strategy may be to enhance varietal diversity, while in other cases it may be most advantageous to promote one particularly productive or pest resistant crop variety.

In both the morphology and color experiment, we found strong evidence that identity effects, rather than varietal richness, drive pest abundance and crop damage in *B. oleracea* mixtures. Despite these effects on crop damage, we found no significant effect of varietal mixtures on crop yield, presumably because plants were able to compensate for this level of crop damage (Trumble et al. 1993). These findings were consistent across two crop traits, morphology and color. Interestingly, while *P. xylostella* responded to intraspecific crop variation in both the morphology and color experiment, we only observed an effect of varietal mixtures on *P. rapae* in the morphology experiment. The outcomes of our study should encourage thoughtful selection of varieties in production systems, as we demonstrate that incorporating particularly influential varieties can dictate plot-level pest dynamics.

In the morphology experiment, we found significantly higher pest abundance and crop damage in plots with broccoli compared to plots without broccoli, and significantly lower pest abundance and crop damage in plots with kale compared to plots without kale. In contrast, we found no effect of morphological richness. These findings provide strong evidence that identity effects are responsible for the observed variation in pest abundance and crop damage across varietal mixtures in our morphology experiment. We suggest that variation in plant architecture could contribute to the contrasting effects of broccoli and kale on pest dynamics (Cuddington and Yodzis 2017). The tightly clumped florets that comprise a head of broccoli may impede natural enemies locating pest larvae and eggs compared to the more open leaf structure of kale. In our study region, *P. rapae* and *P. xylostella* are hosts for several parasitoid species (Shelton et al. 2002), which have been shown to effectively suppress lepidopteran populations in brassica crops (Pimentel 1961a, Talekar and Shelton 1993, Herlihy et al. 2012b). Indeed, there is evidence that variation in plant morphology across *B. oleracea* varieties can affect the ability of

cruciferous pests to hide from natural enemies (Pimentel 1961b). Therefore, the complex architecture of broccoli relative to kale may have reduced biocontrol services in plots where broccoli was present. Insect pests can also differentiate between shades of a particular color. For example, green-yellow wavelengths tend to be more attractive to *P. rapae* adults than blue-green wavelengths (Kelber 2001). Thus, slight variations in the wavelength of the green kale variety and the green broccoli variety may have also contributed to the opposing effects of these varieties on pest dynamics.

Similar to the results from the morphology experiment, identity effects mediated differences in pest abundance and crop damage across mixture combinations in the color experiment. However, intraspecific color variation only affected the abundance of *P. xylostella* larvae; we found no effect of color variation on *P. rapae* larvae or eggs, or *P. xylostella* pupae. Specifically, *P. xylostella* larvae were significantly more abundant in plots with green cauliflower (Vitaverde) than in plots without this variety. This effect translated into significantly higher crop damage in plots where green cauliflower was present compared to plots where it was absent. Previous studies have demonstrated that plant color is one of the most important host finding cues for *P. rapae* (Radcliffe and Chapman 1966, Dunn and Kempton 1976, Jankowska 2006, Tsuji and Coe 2014). Therefore, it is somewhat surprising that *P. rapae* did not respond to intraspecific color variation in our study. We offer two potential explanations. The three cauliflower varieties we selected had different head colors, but similar leaf colors. It is possible that leaf color is a more important crop trait than head color for *P. rapae*. In addition, cauliflower head formation did not begin until the second pest sampling event, which means visual color effects likely did not manifest in time to influence *P. rapae* populations. In contrast to *P. rapae*, olfactory cues appear to play a more important role in host selection by *P. xylostella* (Couty et al. 2006). Plant color can correlate with plant defense compounds (Malenčić et al. 2012, Green et al. 2015), so it is possible that *P. xylostella* was attracted primarily by chemical cues associated with plots where green cauliflower was present. Interestingly, although there was no significant difference in pest abundance in plots with and without white cauliflower (Denali), plots with

white cauliflower had significantly lower levels of crop damage. There was a non-significant reduction in *P. xylostella* abundance in plots where white cauliflower was present, which may have contributed to reduced crop damage.

Contrary to our expectations, we found no effect of varietal mixtures on crop yield in either the morphology or color experiment. This result differs from the findings of a recent meta-analysis demonstrating that varietal mixtures enhanced crop productivity relative to their monoculture components (Reiss and Drinkwater 2018). There are a couple potential explanations for these contrasting results. One, the meta-analysis focused on mixtures of small grains and did not include varietal mixtures of vegetable crops. It is reasonable to assume that the ability of varietal mixtures to support yield services might vary across cropping systems. Moreover, Reiss & Drinkwater (2018) found that cultivar mixtures with four or more varieties had higher yields than mixtures with only two or three varieties. Therefore, it is also possible that our experiments lacked the level of diversity needed to elicit a yield response. Our finding that varietal mixtures did not influence yield is in line with a recent study suggesting that domestication may have limited the ability of crops to over-yield in high diversity environments, as many crop varieties have been under long-term selective pressure to achieve maximum yield in monoculture (Chacón-Labela et al. 2019). It is important to note that marketable yield is determined by both crop quantity (yield) and quality (crop damage). While we did not find an effect of mixtures on crop yield, certain combinations of varieties significantly reduced crop damage, which suggests mixtures have the potential to affect profitability.

Overall, we found mixed effects of varietal mixtures on pest control and crop damage in both experiments. In some instances, monocultures outperformed mixtures. Interestingly, this only occurred when mixtures contained the most susceptible variety (i.e., broccoli in the morphology experiment and Vitaverde in the color experiment), which underscores the importance of carefully selecting the varieties included in a mixture. For example, monocultures of cabbage and kale had significantly fewer *P. rapae* eggs than all of the mixtures containing broccoli (Fig. 1a). We also observed significantly fewer pests in monocultures of Denali (white)

compared to three-way mixtures of Denali, Graffiti (purple), and Vitaverde (green) (Fig. 5). In other instances, varietal mixtures were beneficial. For example, growing broccoli with kale significantly reduced crop damage relative to broccoli monocultures (Fig. 3). We found a similar effect in the color experiment where mixtures of Vitaverde and Graffiti had significantly less crop damage compared to monocultures of Vitaverde (Fig. 7). These findings suggest that while monocultures may be superior to mixtures in some instances, they can also be detrimental if the wrong variety is selected.

Despite advantages of monocultures in some scenarios, mixtures can be important for achieving other production goals. By growing varieties with different maturation times, farmers can spread out labor demands and extend the harvest period (Clawson 1985), which could be particularly useful for small-scale farmers that rely mostly on manual labor. For example, while cabbage-kale mixtures did not reduce pest abundance or crop damage relative to their component monocultures, this mixture combination could allow farmers to access different markets; cabbage can only be harvested once, whereas kale can be harvested multiple times throughout a growing season. Therefore, production goals other than pest management or yield may motivate growers to implement varietal mixtures.

We tested the relative effects of varietal richness and varietal identity across two crop traits, morphology and color, which influence cruciferous pests (Pimentel 1961b, Jankowska 2006, Ahuja et al. 2011). However, *B. oleracea* crops vary in many traits important to plant resistance against insect pests, such as leaf texture and chemical profiles (Ahuja et al. 2011, Peterson et al. 2016), and we did not explore their role. Most research on plant functional diversity has focused on interspecific plant diversity (Hooper et al. 2005), while relatively few studies have explored which crop traits are responsible for plant intraspecific diversity effects on insect herbivores (Abdala-Roberts et al. 2016, Moreira et al. 2016). We recommend future studies vary the level of functional trait richness separately from varietal richness to elucidate the effect of functional trait diversity in varietal mixtures.

Our finding that varietal identity, rather than varietal richness, mediates pest abundance and crop damage implies that, in this system, management strategies that enhance the abundance of influential varieties will be more effective than those focused on maximizing diversity per se. Therefore, to leverage the services that can be provided by varietal mixtures, we should strive to identify and manage the right kind of diversity. However, maintaining varietal diversity remains important for preserving sources of genetic diversity that may be important in the development of future crop varieties. For instance, maintaining a high diversity of crop traits increases adaptability to climatic or biotic stresses by preserving desirable traits such as drought tolerance or pest resistance for crop breeding. Moreover, there is evidence that species with a co-selection history in diverse mixtures maximize functional trait divergence and exhibit stronger biodiversity effects compared to species selected for in simplified systems (Zuppinge-Dingley et al. 2014). Therefore, current simplified crop breeding schemes may be limiting our ability to achieve biodiversity effects in modern day crops (Chacon-Labelle et al. 2019). Re-establishing genetic variation in breeding programs could strengthen the development of traits that contribute to pest-resistance and productivity, and enhance ecosystem services in varietal mixtures (Chacon-Labelle et al. 2019).

REFERENCES

- Abdala-Roberts, L., Berny-Mier y Terán, J. C., Moreira, X., Durán-Yáñez, A., & Tut-Pech, F. (2015). Effects of pepper (*Capsicum chinense*) genotypic diversity on insect herbivores. *Agricultural and Forest Entomology*, *17*(4), 433–438. doi:10.1111/afe.12125
- Abdala-Roberts, L., Hernández-Cumplido, J., Chel-Guerrero, L., Betancur-Ancona, D., Benrey, B., & Moreira, X. (2016). Effects of plant intraspecific diversity across three trophic levels: Underlying mechanisms and plant traits. *American Journal of Botany*, *103*(10), 1810–1818. doi:10.3732/ajb.1600234
- Ahuja, I., Rohloff, J., & Bones, A. M. (2011). Defence Mechanisms of Brassicaceae : Implications for Plant-Insect Interactions and Potential for Integrated. In *Sustainable Agriculture* (Vol. 2, pp. 311–348). doi:10.1051/agro
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1). doi:10.18637/jss.v067.i01
- Cantelo, W. W., & Sanford, L. L. (1984). Insect Population Response to Mixed and Uniform Plantings of Resistant and Susceptible Plant Material. *Environmental Entomology*, *13*, 1443–1445. Retrieved from <http://ee.oxfordjournals.org/content/ee/13/5/1443.full.pdf>
- Capinera, J. L. (2014). Imported Cabbageworm. University of Florida.
- Chacón-Labela, J., García Palacios, P., Matesanz, S., Schöb, C., & Milla, R. (2019). Plant domestication disrupts biodiversity effects across major crop types. *Ecology Letters*, *22*, 1333–1343. doi:10.1111/ele.13336
- Clawson, D. L. (1985). Harvest Security and Intraspecific Diversity in Traditional Tropical Agriculture, *39*(1), 56–67.
- Cook-Patton, S. C., McArt, S. H., Parachnowitsch, A. L., Thaler, J. S., & Agrawal, A. A. (2011). A direct comparison of the consequences of plant genotypic and species diversity on communities and ecosystem function. *Ecology*, *92*(4), 915–923. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/21661554>
- Couty, A., Van Emden, H., Perry, J. N., Hardie, J., Pickett, J. A., & Wadhams, L. J. (2006). The

- roles of olfaction and vision in host-plant finding by the diamondback moth, *Plutella xylostella*. *Physiological Entomology*, *31*(2), 134–145. doi:10.1111/j.1365-3032.2006.00499.x
- Crawford, K. M., & Rudgers, J. A. (2013). Genetic diversity within a dominant plant outweighs plant species diversity in structuring an arthropod community. *Ecology*, *94*(5), 1025–1035.
- Crutsinger, G. M., Collins, M. D., Fordyce, J. a, Gompert, Z., Nice, C. C., & Sanders, N. J. (2006). Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science (New York, N.Y.)*, *313*(5789), 966–8. doi:10.1126/science.1128326
- Cuddington, K., & Yodzis, P. (2017). Predator-Prey Dynamics and Movement in Fractal Environments. *The American Naturalist*, *160*(1), 119. doi:10.2307/3079002
- Dunn, J. A., & Kempton, D. P. H. (1976). Varietal differences in the susceptibility of Brussels sprouts to lepidopterous pests. *Annals of Applied Biology*, *82*, 11–19.
- Green, J. P., Foster, R., Wilkins, L., Osorio, D., & Hartley, S. E. (2015). Leaf colour as a signal of chemical defence to insect herbivores in wild cabbage (*Brassica oleracea*). *PLoS ONE*, *10*(9), 1–20. doi:10.1371/journal.pone.0136884
- Herlihy, M. V., Van Driesche, R. G., Abney, M. R., Brodeur, J., Bryant, A. B., Casagrande, R. A., ... Szendrei, Z. (2012). Distribution of *Cotesia rubecula* (Hymenoptera: Braconidae) and Its Displacement of *Cotesia glomerata* in Eastern North America. *Florida Entomologist*, *95*(2), 461–467. doi:10.1653/024.095.0230
- Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., ... Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, *75*(1), 3–35. doi:10.1890/04-0922
- Hughes, A. R., Inouye, B. D., Johnson, M. T. J., Underwood, N., & Vellend, M. (2008). Ecological consequences of genetic diversity. *Ecology Letters*, *11*(6), 609–23. doi:10.1111/j.1461-0248.2008.01179.x
- Iverson, A. L., Marin, L. E., Ennis, K. K., Gonthier, D. J., Connor-Barrie, B. T., Remfert, J. L., ... Perfecto, I. (2014). Do polycultures promote win-wins or trade-offs in agricultural

- ecosystem services ? A meta-analysis. *Journal of Applied Ecology*, *51*, 1593–1602.
doi:10.1111/1365-2664.12334
- Jankowska, B. (2006). The occurrence of some Lepidoptera pests on different cabbage vegetables. *Journal of Plant Protection Research*, *46*(2), 181–190.
- Jones, T. S., Allan, E., Härril, S. A., Krauss, J., Müller, C. B., & Van Veen, F. J. F. (2011). Effects of genetic diversity of grass on insect species diversity at higher trophic levels are not due to cascading diversity effects. *Oikos*, *120*(7), 1031–1036. doi:10.1111/j.1600-0706.2010.18957.x
- Kelber, A. (2001). Receptor based models for spontaneous color choices in flies and butterflies. *Entomologia Experimentalis et Applicata*, *99*, 231-244.
- Koricheva, J., & Hayes, D. (2018). The relative importance of plant intraspecific diversity in structuring arthropod communities: a meta-analysis. *Functional Ecology*, (February), 1–14.
doi:10.1111/1365-2435.13062
- Lenth, R. V. (2016). Least-Squares Means: The R Package lsmeans. *Journal of Statistical Software*, *69*(1), 1–33. doi:doi:10.18637/jss.v069.i01
- Letourneau, D. K., Armbricht, I., Rivera, B. S., Lerma, J. M., Carmona, E. J., Daza, M. C., ... Trujillo, A. R. (2011). Does plant diversity benefit agroecosystems? A synthetic review. *Ecological Applications : A Publication of the Ecological Society of America*, *21*(1), 9–21.
Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/21516884>
- Long, E. Y., & Finke, D. L. (2014). Contribution of Predator Identity to the Suppression of Herbivores by a Diverse Predator Assemblage. *Environmental Entomology*, *43*(3), 569–576.
doi:10.1603/en13179
- Loreau, A. M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., ... Wardle, D. A. (2001). Biodiversity and Ecosystem Functioning : Current Knowledge and Future Challenges. *Science*, *294*(5543), 804–808.
- Loreau, M., & Hector, a. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, *412*(6842), 72–6. doi:10.1038/35083573

- Macharia, I., Lo, B., & Groote, H. De. (2005). Assessing the potential impact of biological control of *Plutella xylostella* (diamondback moth) in cabbage production in Kenya. *Crop Protection*, 24, 981–989. doi:10.1016/j.cropro.2005.02.005
- Malenčić, D., Cvejić, J., & Miladinović, J. (2012). Polyphenol Content and Antioxidant Properties of Colored Soybean Seeds from Central Europe. *Journal of Medicinal Food*, 15(1), 89–95. doi:10.1089/jmf.2010.0329
- Moreira, X., Abdala-Roberts, L., Rasmann, S., Castagneyrol, B., & Mooney, K. A. (2016). Plant diversity effects on insect herbivores and their natural enemies: Current thinking, recent findings, and future directions. *Current Opinion in Insect Science*, 14, 1–7. doi:10.1016/j.cois.2015.10.003
- Parry, H. R., Macfadyen, S., Hopkinson, J. E., Bianchi, F. J. J. A., Zalucki, M. P., Bourne, A., & Schellhorn, N. A. (2015). Plant composition modulates arthropod pest and predator abundance: Evidence for culling exotics and planting natives. *Basic and Applied Ecology*, 16(6), 531–543. doi:10.1016/j.baae.2015.05.005
- Peterson, J. A., Ode, P. J., Oliveira-hofman, C., Harwood, J. D., Brennan, R., & Birch, A. N. (2016). Integration of Plant Defense Traits with Biological Control of Arthropod Pests : Challenges and Opportunities. *Frontiers in Plant Science*, 7(November), 1–23. doi:10.3389/fpls.2016.01794
- Philips, C. R., Fu, Z., Kuhar, T. P., Shelton, A. M., & Cordero, R. J. (2014). Natural History, Ecology, and Management of Diamondback Moth (Lepidoptera: Plutellidae), with Emphasis on the United States. *Journal of Integrated Pest Management*, 5(3), 1–11. doi:10.1603/ipm14012
- Picasso, V. D., Brummer, E. C., Liebman, M., Dixon, P. M., & Wilsey, B. J. (2011). Diverse perennial crop mixtures sustain higher productivity over time based on ecological complementarity. *Renewable Agriculture and Food Systems*, 26(4), 317–327. doi:10.1017/s1742170511000135
- Pimentel, D. (1961a). An evaluation of insect resistance in broccoli, brussels sprouts, cabbage,

- collards, and kale. *Journal of Economic Entomology*, 54(1).
- Pimentel, D. (1961b). Natural control of caterpillar populations on cole crops. *Journal of Economic Entomology*, 54(5), 889–892.
- Power, A. G. (1988). Leafhopper response to genetically diverse maize stands. *Entomologia Experimentalis et Applicata*, 49(3), 213–219. doi:10.1007/BF00187496
- Power, A. G. (2010). Ecosystem services and agriculture: tradeoffs and synergies. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365(1554), 2959–2971. doi:10.1098/rstb.2010.0143
- R Core Team. (2017). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.r-project.org>
- Radcliffe, E. B., & Chapman, R. K. (1966). Plant resistance to insect attack in commercial cabbage varieties. *Journal of Economic Entomology*, 59, 116–120.
- Reiss, E. R., & Drinkwater, L. E. (2018). Cultivar mixtures: A meta-analysis of the effect of intraspecific diversity on crop yield: A. *Ecological Applications*, 28(1), 62–77. doi:10.1002/eap.1629
- Risch, S. J. (1981). Insect Herbivore Abundance in Tropical Monocultures and Polycultures : An Experimental Test of Two Hypotheses. *Ecology*, 62(5), 1325–1340.
- Ristow, P., Ketterings, Q., Czymmek, K., & Albrecht, G. (2007). Nutrient Management Planning Strategy. *Agronomy Fact Sheet Series*. Cornell University.
- Shelton, A. M., Wilsey, W. T., Hoebeke, E. R., & Schmaedick, M. A. (2002). Parasitoids of cabbage lepidopteran in central New York. *Journal of Entomological Science*, 37(3), 270–271.
- Tahvanainen, J. O., & Root, R. B. (1972). The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia*, 10(4), 321–346.
- Talekar, N. S., & Shelton, A. M. (1993). Biology, Ecology and Management of the Diamondback Moth. *Annual Review of Entomology*, 38(1), 275–302.

doi:10.1146/annurev.ento.38.1.275

Tilman, D., Lehman, C. L., Thomson, K. T., & Thomson, K. T.

(1997). Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences of the United States of America*, 94(5), 1857–61.

doi:10.1073/pnas.94.5.1857

Tilman, David, & Knops, J. M. H. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, 277.

Tooker, J. F., & Frank, S. D. (2012). Genotypically diverse cultivar mixtures for insect pest management and increased crop yields. *Journal of Applied Ecology*. doi:10.1111/j.1365-2664.2012.02173.x

Trumble, J. T., Kolodny-Hirsch, D. M., & Ting, I. P. (1993). Plant Compensation for Arthropod Herbivory. *Annual Review of Entomology*, 38(1), 93–119. doi:10.1146/annurev.ento.38.1.93

Tsuji, J., & Coe, L. (2014). Effects of Foliage Color on the Landing Response of *Pieris rapae* (Lepidoptera: Pieridae). *Environmental Entomology*, 43(4), 989–994. doi:10.1603/EN14084

Wilhoit, L. R. (1992). Evolution of herbivore virulence to plant resistance: influence of variety mixtures. In R. S. Fritz & E. L. Simms (Eds.), *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution and Genetics* (pp. 91–119). Chicago: University of Chicago Press.

Zupinger-Dingley, D., Schmid, B., Petermann, J. S., Yadav, V., De Deyn, G. B., & Flynn, D. F. B. (2014). Selection for niche differentiation in plant communities increases biodiversity effects. *Nature*, 515(7525), 108–111. doi:10.1038/nature13869

Crop damage score	Damage description
0	No damage, or minor leaf damage restricted to a few, small partial holes (leaf tissue is not fully punctured) on the non-harvested portion of the crop
1	A few small holes restricted to the non-harvested portion of the crop
2	Considerable damage to the outer and older leaves, slight damage to the harvested portion of the crop
3	Considerable damage to the outer and older leaves, moderate damage to the harvested portion of the crop
4	Considerable damage to the entire plant, but a portion of plant could still be marketable after damaged areas are removed
5	Severe plant damage that renders the crop unmarketable

Table 3.1. Description of crop damage scoring. Methods based on Macharia et al. (2005).

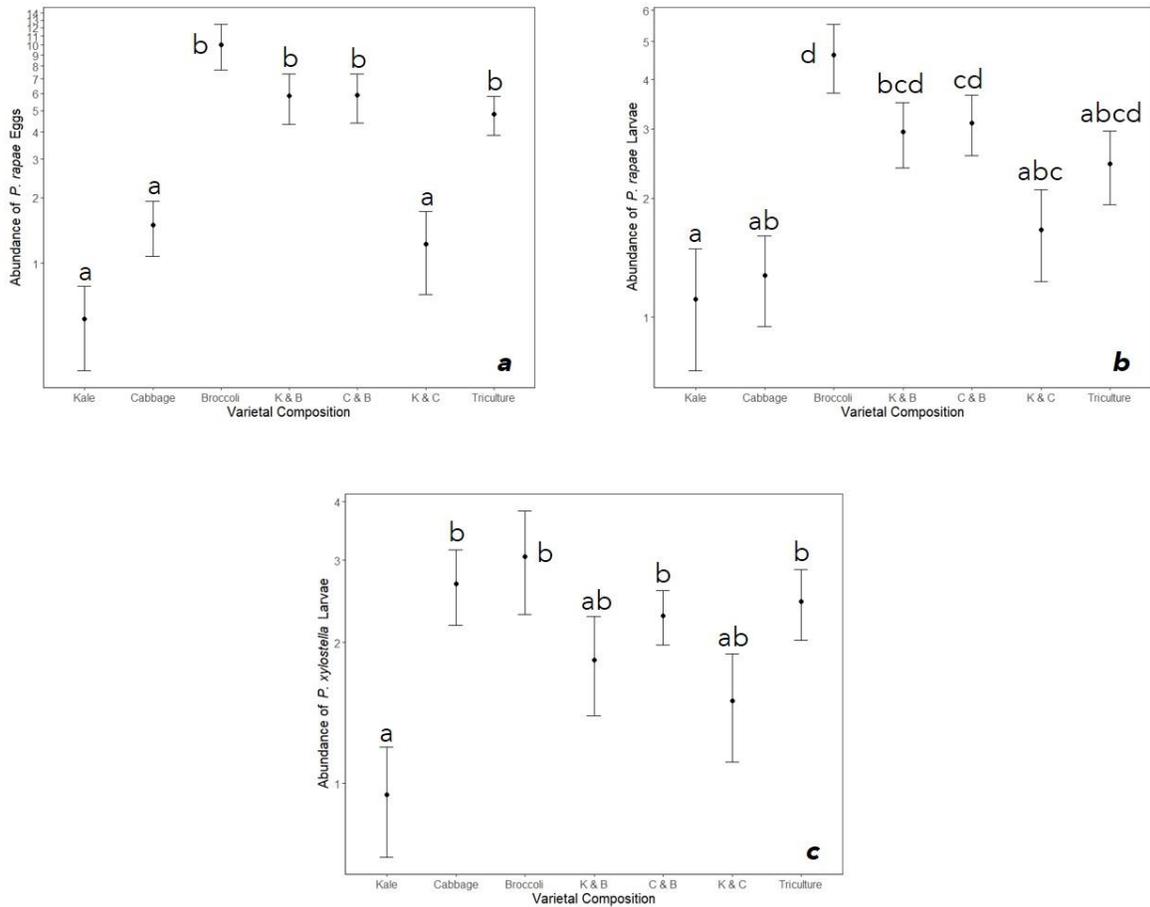


Figure 3.1: The effect of morphological composition on the abundance of *P. rapae* eggs (a) and larvae (b), and *P. xylostella* larvae (c) (mean \pm SE). Means with different letters are significantly different at the $p < 0.05$ level based on least-squares means with a Tukey's adjustment for multiple comparisons. Figure is plotted on the log-transformed scale, but labeled with untransformed values.

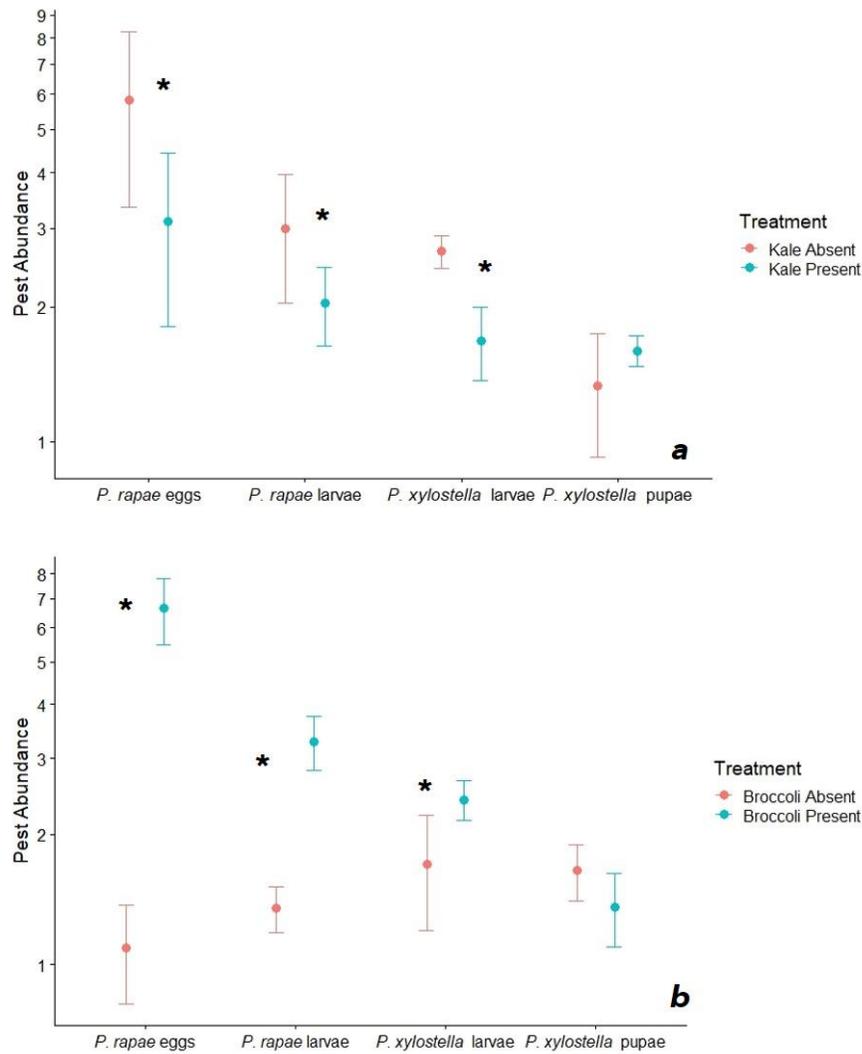


Figure 3.2: The average number of pests in plots where kale is present or absent (a) and where broccoli is present or absent (b). We assessed the effect of the presence of a particular variety by using specific model contrasts to compare the mean of the four treatments with a given variety to the mean of the three treatments without that variety. Values plotted using raw data (means \pm SE) and significance levels determined based on model outputs. Asterisks indicate significant differences in pest abundance at the $p < 0.05$ level.

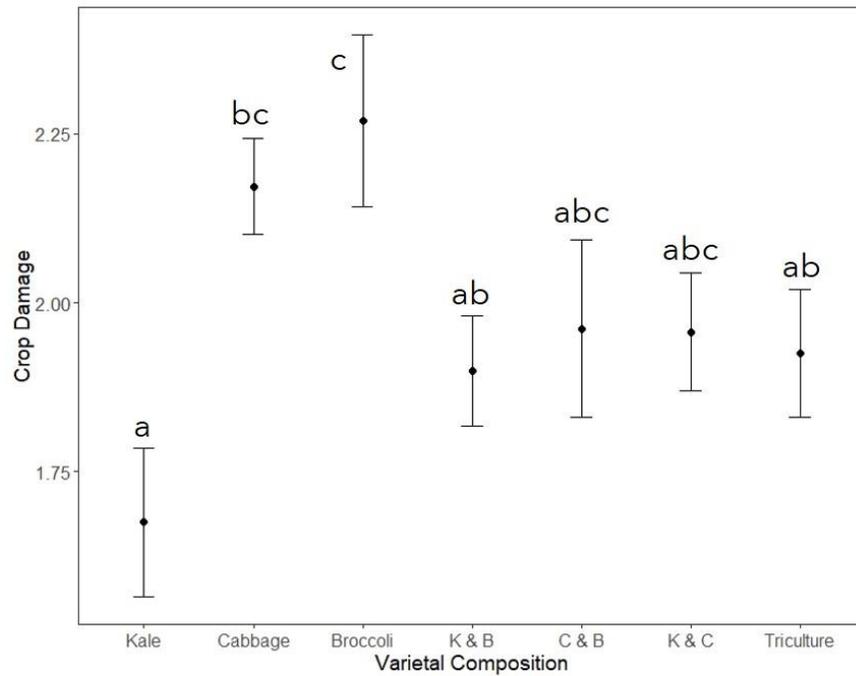


Figure 3.3: The effect of morphological composition on crop damage (mean \pm SE). Means with different letters are significantly different at the $p < 0.05$ level based on least-squares means with a Tukey's adjustment for multiple comparisons.

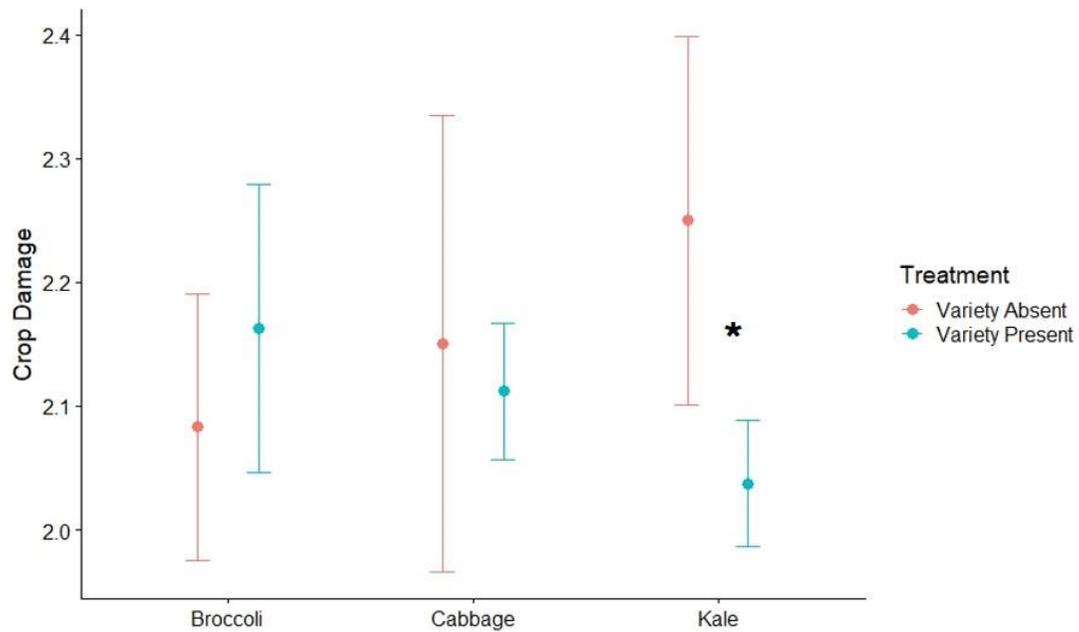


Figure 3.4: Average crop damage when each variety is present or absent. We assessed the effect of the presence of a particular variety by using specific model contrasts to compare the mean of the four treatments with a given variety to the mean of the three treatments without that variety. Values plotted using raw data (means \pm SE) and significance levels determined based on model outputs. Asterisks indicate significant differences in crop damage at the $p < 0.05$ level.

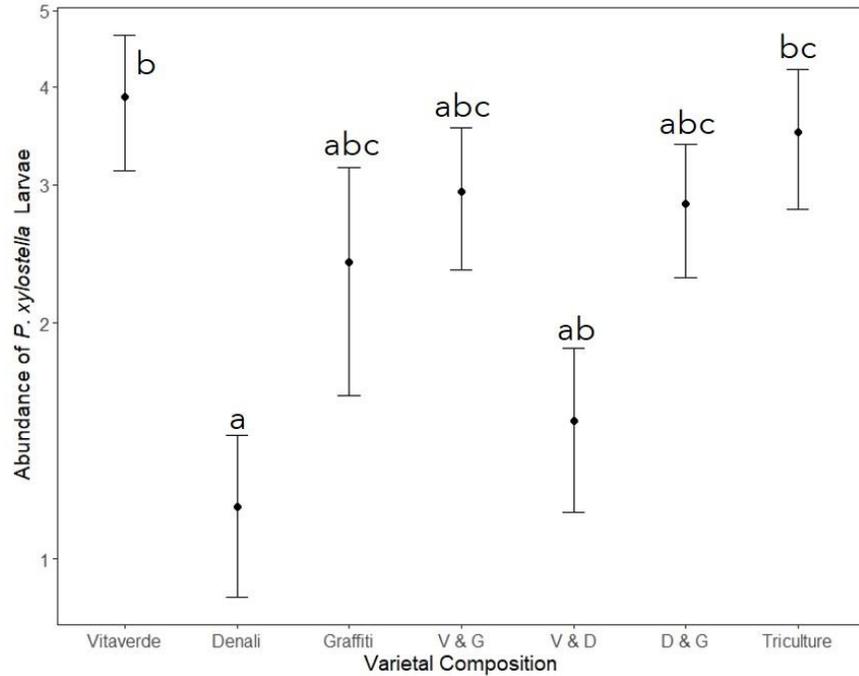


Figure 3.5: The effect of color composition on the abundance of *P. xylostella* larvae (mean \pm SE). Means with different letters are significantly different at the $p < 0.05$ level based on least-squares means with a Tukey's adjustment for multiple comparisons. Figure is plotted on the log-transformed scale, but labeled with untransformed values.

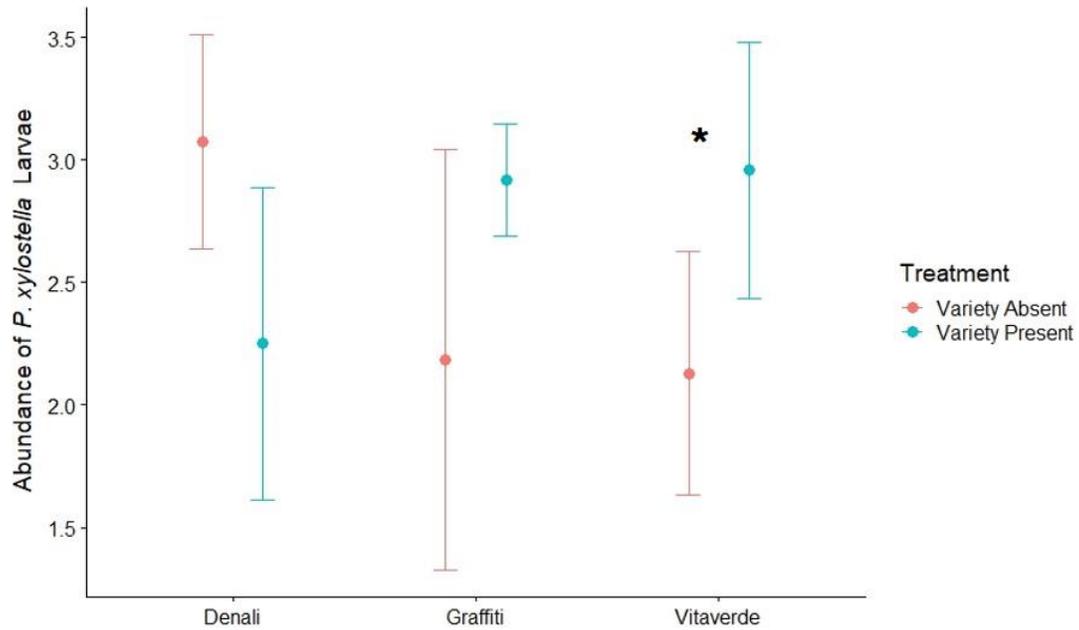


Figure 3.6: The average number of *P. xylostella* larvae when each variety is present or absent.

We assessed the effect of the presence of a particular variety by using specific model contrasts to compare the mean of the four treatments with a given variety to the mean of the three treatments without that variety. Values plotted using raw data (means \pm SE) and significance levels determined based on model outputs. Asterisks indicate significant differences in pest abundance at the $p < 0.05$ level.

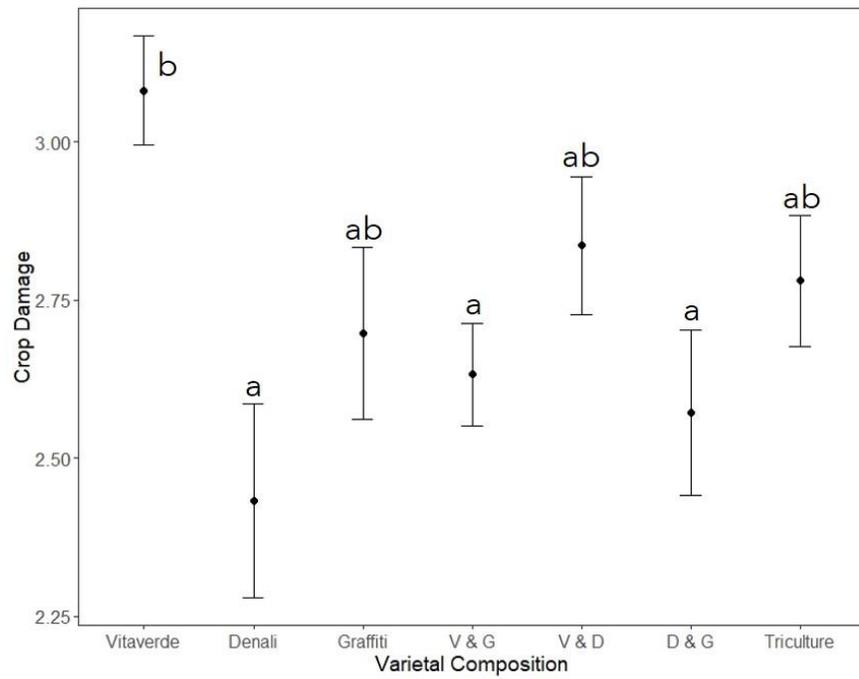


Figure 3.7: The effect of color composition on crop damage (mean \pm SE). Means with different letters are significantly different at the $p < 0.05$ level based on least-squares means with a Tukey's adjustment for multiple comparisons.

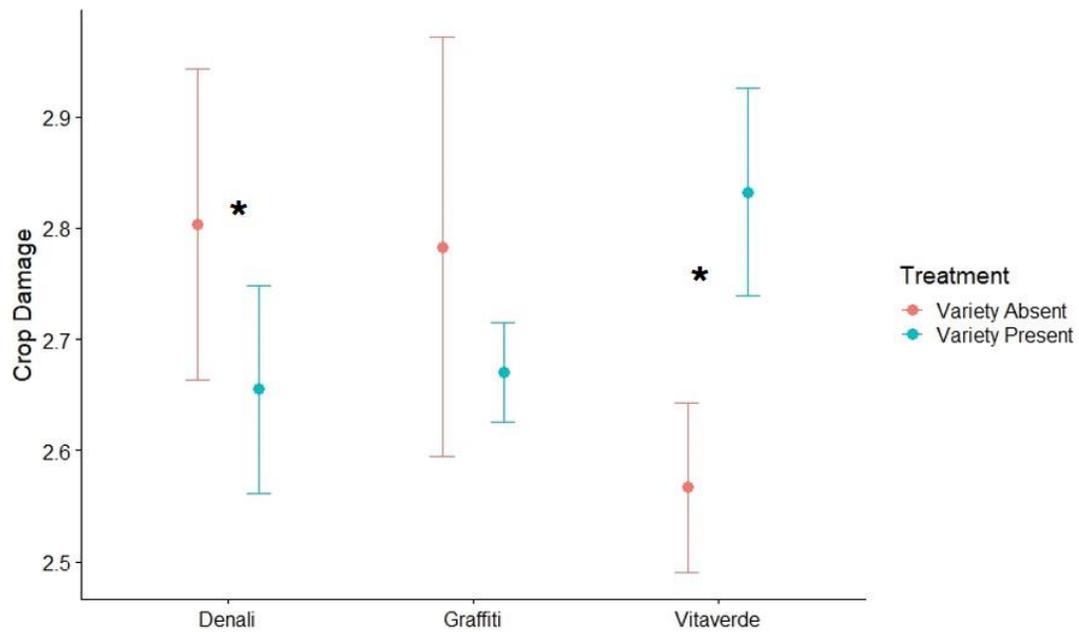


Figure 3.8: Average crop damage when each variety is present or absent. We assessed the effect of the presence of a particular variety by using specific model contrasts to compare the mean of the four treatments with a given variety to the mean of the three treatments without that variety. Values plotted using raw data (means \pm SE) and significance levels determined based on model outputs. Asterisks indicate significant differences in crop damage at the $p < 0.05$ level.

APPENDIX

Chapter 2 Supplementary Material

Input Categories		
Fertility	Pest	Weed
Blood meal	Entrust	Hay
Chicken manure	Protectnet	Straw bale mulch
Feather meal	Pyganic	Weed cloth
Foliar kelp extract	Row cover	Wood chips
Green sand		
Organic compost		
Organic fish emulsion		
Organic phosphorus fertilizer		

Table 2.S1: List of inputs included in the crop budget analysis. These inputs are representative of those used across all farms included in the study.

Crop damage score	Damage description
0	No damage, or minor leaf damage restricted to a few, small partial holes (leaf tissue is not fully punctured) on the non-harvested portion of the crop
1	A few, small holes restricted to the non-harvested portion of the crop
2	Considerable damage to the outer and older leaves, slight damage to the harvested portion of the crop
3	Considerable damage to the outer and older leaves, moderate damage to the harvested portion of the crop
4	Considerable damage to the entire plant, but a portion of plant could still be marketable after damaged areas are removed
5	Severe plant damage that renders the crop unmarketable

Table 2.S2: Description of crop damage scoring. Methods based on Macharia et al. (2005).

CROPLAND			
Season	Scale (m)	r	Significance
Early Season	500	0.1	0.16
Early Season	1000	0.14	0.14
Early Season	1500	0.14	0.18
Late Season	500	0.11	0.85
Late Season	1000	0.11	0.7
Late Season	1500	0.07	0.45

Table 2.S3: Test of spatial autocorrelation of percent cropland at farm sites within three spatial scales (500, 1000, and 1500 m) in the early and late season. Shown are the results of Mantel tests that analyze the relationship between the Euclidean distance of sites—based upon latitude and longitude—and the difference in percent cropland at each spatial scale.

Season	Response Variable	r	Significance
Early Season	Flea beetle abundance	0.009	0.33
Early Season	Crop Damage	0.21	0.08
Late Season	<i>P. rapae</i> larval abundance	-0.09	0.88
Late Season	Crop Damage	0.03	0.29

Table 2.S4: Results of Mantel tests to evaluate spatial autocorrelation between farm fields and response variables in the early and late season.

			VARIETAL RICHNESS		COLOR RICHNESS		PERCENT CROPLAND		VARIETAL RICHNESS X CROPLAND		COLOR RICHNESS X CROPLAND	
Response Variable	Explanatory Scale (m)	Model AIC	estimate	P	estimate	P	estimate	P	estimate	P	estimate	P
Early Season	500	1272.5	3.450	0.035	0.184	0.953	20.094	0.167	-9.902	0.020	-1.803	0.846
Flea Beetle	1000	1269.7	4.642	0.011	-1.588	0.642	18.795	0.121	-12.845	0.007	3.109	0.743
Incidence	1500	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Early Season	500	5308.8	0.551	0.268	-0.326	0.770	0.749	0.895	-1.493	0.247	0.885	0.798
Flea Beetle	1000	5307.4	0.854	0.134	-0.782	0.488	0.228	0.956	-2.259	0.129	2.111	0.503
Abundance	1500	5308.1	0.791	0.193	-0.665	0.561	0.983	0.818	-2.016	0.187	1.551	0.625
Late Season	500	1306.6	-2.543	0.002	-0.222	0.921	-21.126	0.133	6.993	0.004	-0.802	0.915
<i>P. rapae</i>	1000	1310.9	-1.724	0.027	-0.112	0.949	-11.403	0.273	4.459	0.055	-2.111	0.691
Incidence	1500	1312.7	-1.362	0.079	0.196	0.907	-5.442	0.611	3.513	0.151	-3.304	0.555
Late Season	500	954.2	0.087	0.646	-1.353	0.001	-6.687	0.015	-0.283	0.618	3.724	0.009
<i>P. rapae</i>	1000	956.5	0.043	0.834	-1.000	0.023	-4.489	0.088	-0.079	0.893	2.165	0.112
Abundance	1500	957.9	0.115	0.59	-0.828	0.056	-2.968	0.249	-0.325	0.616	1.814	0.209

Table 2.S5: Effect of local-scale predictors (varietal richness and color richness), percent cropland, and the two-way interactions between the local-scale predictors and percent cropland on the incidence and abundance of flea beetles and *P. rapae*. Results from the Binomial model (incidence) and the Poisson model (abundance) evaluating the effect of intraspecific crop diversity and landscape composition on pest incidence and abundance. Bold type highlights significant p-values and lowest AIC values, indicating the most predictive spatial scale.

Response variable	VARIETAL RICHNESS		COLOR RICHNESS		
	Estimate	Uncorrected p values	Estimate	Uncorrected p values	Corrected p values
Profitability	-0.580	0.421	1.848	0.014	0.042
Revenue	0.064	0.855	0.289	0.002	0.008
Labor Cost	-0.014	0.542	-0.034	0.033	0.066
Input Cost	-0.471	0.312	-0.457	0.068	0.068

Table 2.S6: Effect of varietal richness and color richness on profitability, revenue, labor costs, and input costs. Results from linear mixed effects models evaluating the potential for intraspecific crop diversity to support economic services for growers. Bold type shows significant p-values.

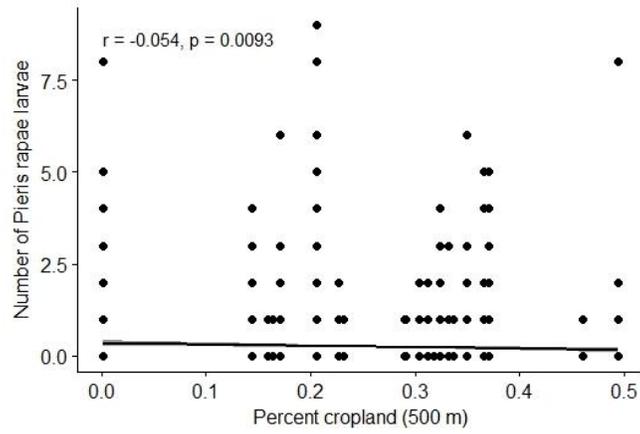


Figure 2.S1: The relationship between percent cropland (500 m) and the abundance of *P. rapae* larvae.

Chapter 3 Supplementary Material

Morphological Richness						
Response Variable	Numerator df	Denominator df	SS	F	P	
<i>Pieris rapae</i> eggs	2	121	3.61	2.6	0.08	
<i>Pieris rapae</i> larvae	2	116	1.09	1.47	0.23	
<i>Plutella xylostella</i> larvae	2	116	0.64	0.97	0.38	
<i>Plutella xylostella</i> pupae	2	123	0.38	0.55	0.58	
Crop damage	2	116	0.75	2.44	0.09	
Crop yield	2	34.19	0.18	0.48	0.62	

Table 3.S1: Results (F-statistics with degrees of freedom, sum of squares, and P-values) from linear mixed models testing for the effect of morphological richness on arthropod pest abundance, crop damage, and yield.

Morphological Composition					
Response Variable	Numerator df	Denominator df	SS	F	P
<i>Pieris rapae</i> eggs	6	117	39.29	15.88	<0.001
<i>Pieris rapae</i> larvae	6	112	10.70	6.00	<0.001
<i>Plutella xylostella</i> larvae	6	112	6.34	3.62	<0.01
<i>Plutella xylostella</i> pupae	6	119	3.70	1.88	0.09
Crop Damage	6	153	5.37	5.83	<0.001
Crop Yield	6	30	1.10	1.01	0.44

Table 3.S2: Results (F-statistics with degrees of freedom, sum of squares, and P-values) from linear mixed models testing for the effect of morphological trait composition on arthropod pest abundance, crop damage, and yield.

Color Richness					
Response Variable	Numerator df	Denominator df	SS	F	P
<i>Pieris rapae</i> eggs	2	118	0.52	0.42	0.66
<i>Pieris rapae</i> larvae	2	118	0.10	0.08	0.92
<i>Plutella xylostella</i> larvae	2	118	1.25	1.26	0.29
<i>Plutella xylostella</i> pupae	2	123	0.21	0.42	0.66
Crop damage	2	118	0.17	0.33	0.72
Crop yield	2	34	0.39	1.04	0.36

Table 3.S3: Results (F-statistics with degrees of freedom, sum of squares, and P-values) from linear mixed models testing for the effect of color richness on arthropod pest abundance, crop damage, and yield.

Color Composition						
Response Variable	Numerator df	Denominator df	SS	F	P	
<i>Pieris rapae</i> eggs	6	112	2.72	0.92	0.48	
<i>Pieris rapae</i> larvae	6	112	1.10	0.64	0.70	
<i>Plutella xylostella</i> larvae	6	112	8.30	3.45	<0.01	
<i>Plutella xylostella</i> pupae	6	117	1.39	1.27	0.28	
Crop damage	6	112	468	4.71	<0.001	
Crop yield	6	30	0.87	0.74	0.62	

Table 3.S4: Results (F-statistics with degrees of freedom, sum of squares, and P-values) from linear mixed models testing for the effect of color trait composition on arthropod pest abundance, crop damage, and yield.