Divided Culture: Integrating and Conservation Biology Agriculture

John Banks
University of Washington Tacoma, jebanks@csumb.edu

Follow this and additional works at: https://digitalcommons.tacoma.uw.edu/ias_pub
Part of the Agricultural and Resource Economics Commons, and the Natural Resources and Conservation Commons

Recommended Citation
Banks, John, "Divided Culture: Integrating and Conservation Biology Agriculture" (2004). SIAS Faculty Publications. 3.
https://digitalcommons.tacoma.uw.edu/ias_pub/3

This Article is brought to you for free and open access by the School of Interdisciplinary Arts and Sciences at UW Tacoma Digital Commons. It has been accepted for inclusion in SIAS Faculty Publications by an authorized administrator of UW Tacoma Digital Commons.
For a conservation biologist, the word “agriculture” conjures up images of slashed and burned landscapes, drifting pesticides, and genetic anomalies that threaten the natural world on many fronts. From a farmer’s perspective, the weight conservation biology places on wildlife may seem overly idealistic and naive, detached from economic and sociopolitical reality. In fact, these endeavors are two sides of the same coin, with a shared heritage in decades of population and community ecological theory and experimentation. Better integration of the two disciplines requires acknowledging their various goals and working to produce mutually beneficial outcomes. The best examples of this type of integrated approach result from careful implementation of sustainable agriculture practices that support biological conservation efforts via habitat amelioration or restructuring. Successful integrated approaches take into account both the environmental and economic costs of different farming schemes and compensate farmers for the costs they incur by implementing environmentally friendly farming strategies. Drawing primarily from examples in insect population dynamics, this paper highlights some innovative programs that are leading the way towards a more holistic integration.

In a nutshell:

- Agriculture and conservation biology seem opposed in their goals and approaches yet share a common ecological heritage
- Communication and cooperation between the two fields are vital for achieving mutual benefits
- More holistic approaches that incorporate a landscape perspective, economics, pesticide use, and the results of empirical and theoretical work should be applied at the interface of agriculture and conservation biology research
- Innovative research and incentive programs worldwide point the way towards better integration of conservation and agriculture

Production agriculture, with its implied ecosystem simplification, pesticide and fertilizer use, and emphasis on yield, often appears to be at odds with conservation biology. From a farmer’s perspective, the weight conservation biology places on wildlife may seem overly idealistic and naive, detached from economic and sociopolitical reality. In fact, these endeavors are two sides of the same coin, with a shared heritage in decades of population and community ecological theory and experimentation. Better integration of the two disciplines requires acknowledging their various goals and working to produce mutually beneficial outcomes. The best examples of this type of integrated approach result from careful implementation of sustainable agriculture practices that support biological conservation efforts via habitat amelioration or restructuring. Successful integrated approaches take into account both the environmental and economic costs of different farming schemes and compensate farmers for the costs they incur by implementing environmentally friendly farming strategies. Drawing primarily from examples in insect population dynamics, this paper highlights some innovative programs that are leading the way towards a more holistic integration.

Scientific publications on agricultural research in the US as early as the mid-19th century clearly recognized the potential benefits of full integration of agriculture and conservation efforts: “If forests, in their primitive state, supply food to birds and insects, or afford shelter to larger animals or reptiles, in a civilized country [they] may be expected to abound more or less wherever there are trees and shrubs to supply them with food and shelter” (Anonymous 1842).

Unfortunately, until only a few decades ago, scientists seem to have strayed from this holistic perspective. For most of the 20th century, relatively few agricultural research projects explicitly focused on the incorporation of non-farmland resources into croplands, except in cases that might strictly benefit agricultural production. Until recently, government agencies in the US (eg the Soil Conservation Service – now the USDA Natural Resources Conservation Service) were more concerned with conservation as a means of minimizing erosion and its effects on public works projects than on preserving biodiversity. For their part, conservation biologists, frequently under pressure to produce timely responses to crises, have often overlooked the fact that agricultural ecosystems represent a sizable proportion of global terrestrial landscapes (eg over 50% of the European Union landscape and close to 70% of Denmark and Bangladesh), and have largely failed to incorporate them into research and policy-setting activities. Despite these differences in focus, a close look at the ecological basis for many aspects of agriculture and biological conservation reveals striking similarities. Both disciplines are concerned with managing natural resources based on societal mandates: agriculture...
Integrating agriculture and conservation

focuses on production food and fiber crops, whereas conservation efforts generally focus on the maintenance of biological diversity. Both of these endeavors require a deep understanding of population dynamics, community ecology, and the effects of spatial scale and disturbance on biotic communities. Fortunately, scientists and practitioners alike have recently been making progress in recognizing these similarities, and have integrated them in creative and innovative ways.

This paper explores some of the similarities and differences in the perspectives of these two disciplines, and describes some examples that are paving the way to integration. Because insect population dynamics studies abound in both agricultural and conservation biology research, these studies will be used to illustrate comparisons between the two fields.

A shared heritage: experiments and theory

Habitat heterogeneity

Much of what we know about how populations and communities of plants and animals interact stems from experiments conducted in agricultural settings, which are relatively simple and easy to manipulate. Work exploring how habitat diversity (or heterogeneity) may influence resident organisms has generated insights that are especially valuable to both agriculture and conservation biology. Root’s (1973) early field experiments in flea beetle-collard systems have stimulated much empirical and theoretical work to test the idea that diversified planting schemes may thwart insect herbivores seeking to colonize and invade host plants. Building on earlier ecological work (e.g., Elton 1927), Root and others demonstrated that more diverse environments may attract a broader array of predators and parasitoids, enhancing prey control and fostering biodiversity (Root 1973; Andow 1991). In the three decades following Root’s pioneering insect work, there has been much ado about vegetation diversity and spatial arrangements of vegetation and other resources in applied agriculture. Results from these studies have been embraced by conservation biologists, especially as applied to reserve design and habitat fragmentation (Quinn and Harrison 1988).

A subdiscipline of earlier biological control work, conservation biological control (CBC), has flourished over the past several decades (van den Bosch and Telford 1964; Barbosa 1998). Fueled by increasing awareness of the dangers that alien biological control agents may pose to native non-target species, CBC research is aimed at encouraging native predators and parasitoids of pests species in and around farmlands, usually by manipulating habitat or resources that are important to these organisms (Landis et al. 2000). Ornamentals and other non-crop plants are often actively sown into crop areas to provide pollen, nectar, and alternative prey for predators and parasitoids (Figure 1). Manipulating habitat effectively is no easy task; some changes may result in increased pest problems due to predator–predator interference or the inadvertent creation of additional resources for pests (Snyder et al. in press). Historically, most CBC studies have focused primarily on the benefits to agricultural production, with little concern for community or regional biodiversity conservation. However, a large body of work conducted over the past 10 years emphasizes the need for a larger, landscape perspective in integrating agricultural pest control and biodiversity considerations (Kruess and Tscharntke 1994; Marino and Landis 1996; Thies and Tscharntke 1999; Östman et al. 2001). Recent studies have focused on identifying the benefits of CBC to biodiversity conservation (see Landis et al. 2000); more support for this type of work is necessary to generate innovative solutions that address both agriculture and conservation concerns.

Metapopulation theory

Many of the quantitative analytical tools commonly employed by ecologists in modern conservation studies were developed with agricultural pest control in mind. Metapopulation theory, which considers species’ survival...
from the perspective of groups of populations, each with their own individual internal dynamics but linked by dispersal, has frequently been used to analyze the viability of rare or endangered species (Gilpin and Hanski 1991) such as the northern spotted owl. This framework was originally formulated for a very different purpose, namely to improve upon ways of eradicating insect pests in agriculture (Levins 1969). This shared heritage, which highlights other influential factors common to the two fields, such as dispersal and resource dynamics, could be used to greater advantage. Although in temperate agroecosystems, insect pest populations often fluctuate in synchrony and therefore do not lend themselves to metapopulation analysis, metapopulation theory has been successfully applied in agroecological studies (eg Landis and Menalled 1998; Hietala-Koivu et al. 2004). Similarly, island biogeographic approaches, famously used in a variety of conservation settings (Quinn and Harrison 1998) rarely receive serious consideration in agroecological circles, although some classic works have outlined applications for herbivorous insects (eg Janzen 1968). The application of theory to agriculture has been most powerful when it inspires direct field tests. For instance, Murdoch et al. (1996) disrupted insect dispersal in an elegant field experiment designed to test whether or not stable scale insect–parasitoid interactions were driven by metapopulation dynamics. There is clearly a need for agroecology research to embrace such theory-based approaches, much in the way that conservation biology has adopted the use of matrix modeling and viability analyses to combat extinction crises.

### Habitat fragmentation, loss, and spatial scale

The habitat alterations associated with agricultural production often have devastating effects on plant and animal populations, and in some cases a cascade of further effects stems from socioeconomic factors. A poignant example lies in tropical fruit and vegetable production. After rainforests are replaced by monocultures, changes in world markets or pathogen outbreaks may result in displaced workers who have little alternative but to clear further forestlands in order to subsistence farm (see Vandermeer and Perfecto 1995).

Apart from these more complex human–environment interactions, combating the combined effects of habitat loss and fragmentation poses tremendous challenges. Recent research suggests that while habitat loss often accounts for most of the detrimental effects on biodiversity (Schmiegelow and Monkkonen 2002), the spatial configuration and relative abundance of small and large remnant patches may greatly influence biodiversity and biological control (Kruess and Tscharntke 1994). The details of habitat degradation and loss may be especially critical in understanding declines in pollinator biodiversity across a broad range of taxa (Kremen and Ricketts 2000). For instance, the presence of forest fragments has recently been identified as crucial for bolstering pollinator and subsequent yield in Brazilian coffee agroecosystems (De Marco and Coelho 2004). At issue are taxon-specific habitat requirements and dispersal abilities, which differ even among the members of the same class of organisms. For example, aphids and beetles respond differently to fragmentation of host plants (Kareiva 1987; Banks 1998), and butterflies and beetles respond differently to habitat fragmentation than their respective parasitoids (Kruess and Tscharntke 1994). These and other examples underscore the need to identify and prioritize conservation of particular taxa in landscapes that are mosaics of agricultural and natural areas.

In recent years, the spatial scale at which experiments are conducted has also received much attention in ecological circles (Tilman and Kareiva 1998), yet it is still rare for experiments in both agroecology and conservation biology to explicitly incorporate scale as a treatment factor (but see Marino and Landis 1996; Roland and Taylor 1997; Banks 1998). Recent surveys of how increased vegetation diversity in agroecosystems affects insect pest populations indicate that answers vary with the spatial scale of experimental plots (Bommarco and Banks 2003). This is not surprising; spatial scale critically impacts the dispersal abilities of organisms in a species-specific way, something that conservation biologists have been aware of for a long time (Doak et al. 1992). Given the sensitivity of species interactions to scale, from parasitoid releases to set-aside conservation policies, we need a better understanding of how spatial scale interacts with both biotic and abiotic processes.

### Agricultural lands as habitat

Anyone familiar with tropical ecosystems is aware of the degree to which natural vegetation encroaches upon tropical agricultural habitats (Figure 2). Recent work suggests that agricultural areas in the tropics, often in a mosaic of rainforest fragments, may be important to the conservation of species ranging from mammals to insects (Ricketts et al. 2001; Daily et al. 2003). Similar attention has been paid to temperate agricultural landscapes as bird habitat; several studies – including analyses of set-asides established by England’s Common Agricultural Policy – have indicated that non-crop vegetation structure may greatly influence the suitability of such habitats for wildlife (Firbank et al. 2003). Because it is often prohibitively expensive to eradicate weeds, farmers in the tropics often tolerate weeds or other “volunteer” crop species in their fields. An inadvertent benefit of this, which low-input or organic farmers in the tropics often enjoy, is that planned or unplanned increases in vegetation diversity can lead to increases in beneficial species and reduced chemical inputs (Figure 3).

Conservation biologists have heralded the biodiversity increase associated with lower intensity farming as a step in the right direction (Figure 4) – but which species rep-
resent the right kind of biodiversity? While conservation biologists have been focusing on the importance of functional biodiversity rather than “biodiversity for biodiversity’s sake” for years (see Kareiva and Levin 2003), there is still a tendency within agricultural circles to focus on biodiversity strictly in terms of crop production benefits. Recent work on the threat of invasive species illustrates this difference in perspective. For instance, long-term studies documenting beetle species composition following the introduction of the seven spotted ladybird beetle (*Coccinella septempunctata*) have revealed a decline in native ladybird beetle species in temperate areas in the northern US (Elliott et al. 1996). This decline, however, seems to have been offset by a matching overall increase in ladybird beetle abundance (compensated in part by invasive *C. septempunctata*), with little loss in predation on aphid prey in agricultural systems. As a result, the invading ladybird beetle has been the subject of little concern for farmers; indeed, *C. septempunctata* was introduced for the very purpose of controlling aphid pests, and seems to be doing its job. Why should growers be concerned about a slight decline in native biota associated with its introduction?

One answer comes from the fact that native fauna, both predators and prey, have had a chance to coevolve with their community in a way that introduced organisms (eg imported biological control agents) may not have had. Evidence suggests that native ladybird beetles, for instance, may be more attuned to fluctuations in prey density than their alien counterparts (Evans 2004), increasing their potential for better biological control. In agroecosystem predator–prey relationships, mismatches between native and non-native species are common, for the simple reason that many of our agricultural predators and pests (and crops) were themselves imported from elsewhere. A further complication is the artificial annual cycle imposed on agroecosystem communities by harvest timing and markets. Predators, especially those introduced from elsewhere (as in classical biological control scenarios), are often asynchronous with their insect prey in annual cropping systems (Wissinger 1997); the prey cycle with the annual resource, whereas the predators may be cycling on a longer time scale. Furthermore, when subject to disturbances such as pesticide use, predators and other non-target organisms often fare worse than target species, in part due to longer generation times and lower reproductive rates (Stark et al. 2004). These effects, which are due to co-evolutionary forces and differences in life history strategies, provide a clear argument for the preservation of native species, in both managed and natural settings.

Recent work also suggests that native biodiversity may play a critical role in so-called “ecosystem services” (Daily 1997). In this case, there is a quantifiable link between the loss of biodiversity (in both natural and managed communities) and the sustainability of normal, healthy ecosystem functioning – something that is often not apparent until well after the loss of biodiversity. Similar “farm services” are provided by the agroecosystem biodiversity (Naylor and Ehrlich 1997), though we are yet to fully understand the extent that native biota play in agroecosystem regulation and function.

### Integrated pest management: selective pesticides and cultural controls

Agriculture has run afoul of efforts in biological conservation through the continued widespread use of chemical pesticides. Agricultural inputs have been implicated in a series of both public and environmental health threats in recent years, including endocrine disruption in humans and wildlife (Solomon and Schettler 2000). The rise in environmental consciousness following the publication of Rachel Carson’s book, *Silent Spring*, in 1962 has led to a rich legacy of studies that explored various aspects of sustainable agricultural systems, with an eye towards balancing the maintenance of pest control and biological integrity (Altieri 1995, 2004). This positive focus on sustainable agroecosystems has been accompanied by a tendency within agroecological research to ignore the “elephant in the room” – the fact that pesticide use is still widespread in the US. Despite the passage of the 1996 Food Quality Protection Act (FQPA) by Congress, which mandates that the Environmental Protection Agency...
JE Banks Integrating agriculture and conservation

(EPA) reevaluate nearly 10,000 specific uses of pesticides, growers still rely heavily on chemical controls to regulate insect pests.

An alternative to chemical controls that is nicely aligned with biological conservation is the use of increased vegetation diversity to reduce insect pest populations. This approach allows for the incorporation of more plant species, some of which are important to bird and small mammal populations, into agroecosystems. This technique is thought to reduce colonization of pest insects by making it more difficult for them to find their host plants in a matrix of vegetation, and also to bolster natural enemy populations drawn to the wide array of resources (e.g., pollen, nectar, alternate prey) associated with increased plant diversity (Root 1973). While greater vegetation diversity can be an effective means of pest control, it is by no means a panacea; surveys and meta-analyses indicate that only in a simple majority of cases, increased vegetation diversity in croplands reduces herbivore pressure (Andow 1991; Tonhasca and Byrne 1994). Furthermore, these results are highly dependent on mitigating factors such as the spatial scale of the crop resources, a highly variable factor in agricultural settings (Bommarco and Banks 2003). The inconsistency of vegetation diversity as a pest control technique, coupled with mechanized harvesting, has made it difficult for farmers to rely solely on cultural controls for combating insect outbreaks. Although integrated pest management has been widely used as a strategy for increasing sustainability in commercial farms, research exploring combinations of pesticide use with other forms of pest control such as cultural control (e.g., intercropping) appears to be declining in agroecology research. A brief survey of Agriculture, Ecosystems, and Environment (Elsevier), an international journal devoted to exploring the interface between agricultural and environmental issues, reveals that only 7% of the research articles in a recent volume (2003; Volume 95) explored the effects of pesticide use in their studies. This compares to 44% in a comparable number of articles from 20 years ago (1983; Volumes 9 and 10). This decline in studies incorporating pesticide use with other forms of sustainable farming strategies may simply reflect changes in the agroecology landscape; recent research focuses more on topics such as new technologies (e.g., GIS) and farming innovations in steeplands in remote tropical areas— but nonetheless it is a surprising trend. The loss of many traditional pesticides resulting from the FQPA mandated EPA action has precipitated the development of a suite of new selective pesticides (e.g., imidacloprid) that growers are rapidly incorporating into their pest-management regimes. Real progress in implementing more sustainable farming in the US will require a shift from large-scale,
Integrating agriculture and conservation  JE Banks

heavy-input farming to medium-scale farming that incorporates nature-mimicking processes. A transition period will be necessary, during which farmers will rely on the continued use of increasingly selective pesticides and other inputs. The challenge that faces both conservationist biologists and growers is maximizing yields while minimizing environmental impacts.

Research integrating natural vegetation in croplands and limited selective pesticide sprays illustrates how farmers may be able to decrease pesticide use and still maintain adequate pest control. Lee et al. (2001) demonstrated that non-crop vegetation strips within farming areas might prove useful for offsetting the negative effects of insecticide sprays on predatory carabid beetles. Banks and Stark (2004) conducted a field experiment in which aphids in plots of broccoli surrounded by either weedy margins or bare ground were sprayed with pesticide or surfactant alone. Even exposure to a small amount (one-eighth of the recommended field application rate) of the selective pesticide imidacloprid yielded a major reduction in aphid pest densities (Figure 5). Furthermore, increased vegetation diversity acted synergistically with selective pesticide sprays, with pest densities in weedy plots dropping by only 4% when no pesticide was sprayed, but down by 40% on average 4 days after pesticide spraying (skew lines in Figure 5). These kinds of results highlight the need for further experiments combining cultural and chemical controls as a bridge between organic and conventional farming.

Genetically modified organisms: déjà vu?

A discussion of the interface between agriculture and conservation would be incomplete without considering the impact that genetically modified organisms (GMOs) will likely have in both areas. Touted more than a decade ago as a means of potentially decreasing the use of herbicides and pesticides, increasing yields, and creating crops adapted to marginal habitats that would reduce pressure to convert other habitat for agriculture (OTA 1991), GM crops are now being seriously evaluated in terms of overall effects on agroecosystem communities (see Firbank 2003 and other articles in the same volume).

As noted in a recent editorial in this journal (Silver 2003), the results from a series of trials conducted in the UK indicate that the environmental benefits stemming from the use of genetically modified crops may not be as great as originally purported. At the same time, a recent debate over the potential for GM crops to negatively affect nymphalid butterflies and other non-target organisms has now subsided as a slate of recent field studies illustrate that such threats are minimal (Koch et al. 2003). Lessons learned from these and other GMO introductions have inspired greater vigilance worldwide, as the specter of increasing numbers of GMOs released into the natural landscape looms large on the horizon. In particular, concerns remain about transgene escape into non-cultivated wildlands and widespread resistance to endotoxins and herbicides (Hails 2002).

Conservation biologists have good reason to fret over these potentially devastating environmental impacts, as they conduct what is arguably one of the largest uncontrolled experiments ever conducted in field community ecology. Growers and conservation biologists have different stakes in this experiment: growers are concerned about frittering away a potentially powerful technology, whereas conservation biologists are struggling to predict how widespread deployment of transgenes such as Bt endotoxin will affect the natural environment. Both camps would benefit from more discussion and interaction, as the ultimate goal is to increase the sustainability of food production while also increasing environmental protection through decreased inputs. A positive sign is the recent establishment of policies recommending 20% non-trans-
Getting it right: interdisciplinary approaches

Arguably, the best chances for bolstering both conservation and agriculture lie in gathering information across several scales: at the local level, understanding values and motives for stakeholders; at the landscape level, understanding biotic and abiotic forces and cycles; and at the national and international levels, understanding how policies and incentives play out at the other scales. Over seven decades after Weaver's (1927) early article in *Ecology*, considering Midwestern agriculture in the context of the prairie ecosystem, a proliferation of articles and books highlighting the need to render farming efforts more harmonious with the natural environment offer more holistic approaches to integrating agriculture and conservation (eg Landis and Menalled 1998; Thies and Tscharntke 1999; Östman et al. 2001; Jackson and Jackson 2002). Innovative programs that demonstrate a shift in focus from a single species to landscape and regional conservation efforts are springing up worldwide. In Australia, a recent comprehensive terrestrial conservation plan was the result of a cooperative effort to assess what it would take, in terms of economics, stakeholder involvement, and public policy to launch a concerted nationwide effort aimed at maintaining and restoring biodiversity to critical regions (NLWRA 2002). It will require integrating agricultural production and biodiversity conservation efforts; in some regions (eg Western Australia), historical land-clearing practices and cumulative salinization have rendered conservation progress extremely unlikely. In regions where yields and farming profit margins are low, government incentives will probably be needed to offset the economic disincentives perceived by farmers (NLWRA 2002). This sort of analysis, comprehensive in both scope and perspective, is a step in the right direction. The challenge remains to involve farmers (who manage about 60% of Australia’s land) and to make them feel they have a vested interest in the conservation outcomes (NLWRA 2002).

Elsewhere, researchers from universities, governments, and non-profit agencies are experimenting with similar support systems for more conservation-oriented farming. In the neotropics, much recent research has documented the benefits of shade-grown coffee for arthropod, bird, and mammal conservation (see Somarriba et al. 2004). Shade grown certification programs sponsored by the Audubon Society and others have provided economic support for further conversion from sun to shade-grown coffee, as have suggestions from recent research that shade-grown coffee actually tastes better (Roubik 2002).

In the US, the Nature Conservancy has been working with farmers in central California to increase on-farm resources for migratory birds. Using combinations of conservation tillage, sheep grazing, and flooding to control weeds, managers of Staten Island in San Joaquin County have seen marked increases in sandhill cranes and other wildlife (Ivey et al. 2003). Site managers have also made subtle changes in ditch structure and in the timing of waterfowl hunting access and harvesting in order to optimize shared use among humans and wildlife while maintaining agricultural profitability (Ivey et al. 2003).

In the European Union, a key aspect of more than a decade of programs aimed at encouraging farmers to be more environmentally friendly has been financial support for participants. Such strategies have resulted, for instance, in more than 10% of arable land in England being taken out of production to support wildlife—a program that has been particularly effective in providing habitat for breeding birds (Firbank et al. 2003). Critical to the success of such programs is the willingness to compensate participating farmers for potential losses due to habitat and farming practice modifications aimed at fostering wildlife in agricultural lands. Successful national and multi-national cooperative efforts have been moving towards a more progressive model of accounting that tries to incorporate the real costs of environmental degradation due to farming. This innovative approach is similar to recent exemplary corporate models incorporating real environmental costs into business and industry settings (eg Hawken et al. 1999), and continued success will require extensive cooperation among parties with very different worldviews. Early assessments of the efficacy of the EU programs are mixed and have generated substantial controversy (Kleijn et al. 2001), but the existence of such programs suggests we can be more confident about our
abilities to bridge any remaining gaps between conservation and agriculture.

**Conclusions**

Differences in perspective between agriculture and conservation may appear large and irreconcilable at times. However, holistic, multi-scale, interdisciplinary approaches offer the most hope for better aligning the efforts and goals of these two disciplines. Current work bringing a landscape perspective to biological control and conservation in agricultural habitats is forging new alliances among researchers and practitioners from both disciplines. In both agroecological and biological conservation research, it is imperative that we continue to draw upon a shared ecological heritage and deliberately incorporate issues such as habitat heterogeneity, spatial scale, pesticide use, and the anticipated effects of GMOs into field and theoretical investigations. Furthermore, incorporating natural vegetation, mimicking natural systems, integrating community needs and addressing economic issues are all critical elements of mutually beneficial solutions.

**Acknowledgments**

Thanks to G Chang, M Marvier, B Snyder, and D Landis for helpful comments and suggestions. The Helen Riaboff Whiteley Center at Friday Harbor Laboratories on San Juan Island provided lodging and resources during the preparation of this article.

**References**


