

Rove Beetles (Coleoptera, Staphylinidae) as Bioindicators of Change in Boreal Forests and Their Biological Control Services in Agroecosystems: Canadian Case Studies

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Abstract

The Staphylinidae, or rove beetles, is one of the largest and most biologically diverse of the beetle families. The world fauna consists of more than 63,495 described species, with more than 1774 species recorded in Canada. By virtue of their sheer abundance, number of species and trophic diversity, rove beetles play important roles in terrestrial ecosystems. These beetles also have great potential for use as indicators of forest change because of their affinity for specific habitats and microhabitats and their sensitivity to habitat change. With continued advances in identification tools such as taxonomic keys with high-resolution photos, rove beetles have been increasingly incorporated into biodiversity research projects, thus increasing both the scope and inferences drawn from these studies. In this chapter, we highlight recent biodiversity studies using rove beetles and discuss how these beetles have added to our perspectives on changing forest and agroecosystems. In forest ecosystems, rove beetle assemblages are

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affected by both large- and small-scale natural

disturbances, forest succession and silvicul-

dian agroecosystems, rove beetles have mostly been used in conservation biological control as a diverse assemblage of generalist predators or in more focused applications. We provide a review of the research conducted in Canadian agroecosystems and describe general patterns of the communities across a variety of crop types and compare these with other agricultural systems on a global scale. While the temporal and spatial dynamics of rove beetle assemblages

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ture. Thus far in boreal ecosystems, responses of rove beetles have been evaluated primarily in terms of their responses to stand-replacing wildfire and clearcut harvesting. However, given the apparent affinity of rove beetles for microhabitats, increasing attention has been focused on smaller-scale disturbances and silvicultural interventions that may leave residual standing trees, create small gaps and/or modify soils or deadwood. Rove beetles also are important biological control agents against pest populations. In Canadian agroecosystems, rove beetles have mostly

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and the responses of their populations to different cultural practices are becoming better known, direct predator-prey interactions and subsequent impacts on pest populations remain poorly understood. Biological control of several dipteran pests by rove beetle parasitoids in the genus *Aleochara* remains one of the best-studied systems, likely due to the high specificity of *Aleochara* for dipteran hosts. Several general recommendations are provided for future research to better quantify and predict control by rove beetles.

9.1 Introduction

Rove beetles, along with weevils, leaf beetles and ground beetles, are among the largest and most biologically diverse beetle families in Canada and globally (Klimaszewski 2000; Bousquet et al. 2013). Newton et al. (2001) recorded over 46,200 known rove beetle species worldwide; however, there are now more than 63,495 described species in 3,762 genera (Newton, pers. com.). In Canada and Alaska, there are 1682 recorded rove beetle species (Bousquet et al. 2013) in 274 genera and 24 subfamilies (Klimaszewski 2000). Recent taxonomic revisions suggest that the number of described species in Canada and Alaska is now exceeding 1700 species (Webster et al. 2016). Yet, even with recent revisions, many species of the Canadian fauna still remain undescribed or have yet to be recorded from Canada. This is particularly true for the largest rove beetle subfamily, Aleocharinae, which may contain over 700 species in Canada and Alaska.

Rove beetles are readily distinguished morphologically from other Coleoptera. The family is best known for their shortened elytra and elongate flexible abdomen. Most species possess welldeveloped wings and good dispersal abilities (Halder 2011). Some (e.g. Aleocharinae) have developed defensive glands with chemicals to deter predators (Klimaszewski 2000). The majority of adults are nocturnal and generally avoid contact with light and prefer moist habitats like forest litter.

Many rove beetles (e.g. some Aleocharinae, Staphylininae, Paederinae, Scydmaeninae) are predators of other arthropods, but examples of other feeding relationships such as fungivory and herbivory are known. Gyrophaenina species are exclusively mycophagous, feeding on fungal spores and hyphae (Ashe 1984). Likewise, all species within the Scaphidiinae are obligate or facultative inhabitants and consumers of fungi (Newton 1984). A number of species are saprophagous and feed mainly on decomposing organic material (some Oxytelinae and Osoriinae) or are phytophagous on pollen, algae and rarely the leaves and stems of higher plants (some Omaliinae, Osoriinae, Oxytelinae) (Klimaszewski 2000; Frank and Thomas 1991). Larvae of Aleochara species are ectoparasitoids on pupae of cyclorrhaphous Diptera (Klimaszewski 1984). Some species occur under the bark of trees or logs (e.g. Anomognathus, Dexiogyia, Homalota, some Leptusa, Placusa) and may be predaceous or fungivorous (Klimaszewski et al. 2016a). Many other species are affiliated with ants (some members of Athetini, Oxypodini and Lomechusini). The primary feeding modes (trophic affiliations) of rove beetles are presented in Klimaszewski (2000) and Thayer (2005). However, information on feeding habits of many rove beetles is still expanding. For example, many species of the aleocharine tribe Athetini were historically considered predaceous, but this assumption was based on little empirical evidence. Recent molecular and microscopic analysis of the gut contents of abundant rove beetles (indicators of mature forests), including several athetine species in the boreal balsam fir forest of eastern Canada, revealed a lack of arthropod fragments or arthropod DNA in their posterior guts but presence of a diverse fungal community dominated by yeasts (Klimaszewski et al. 2013a; Stefani et al. 2016). Predominance of yeasts and fungal spores in the posterior gut of rove beetles suggests that fungi may play an important role in rove beetle dietary requirements and as endosymbionts (Klimaszewski et al. 2013b; Stefani et al. 2016).

High species richness, diversity of trophic relationships and sensitivity to changes in environmental conditions and microhabitats suggest that rove beetles may serve as useful ecological indicators and provide a large suite of potentially significant species in biological control efforts. In Sects. 9.2–9.8, we provide a short review of recent studies that have used rove beetles to evaluate the ecological impacts of different approaches to forest management. These examples come largely from boreal forests. In Sects. 9.9–9.13, we provide a review of the research conducted in Canadian agroecosystems and describe general patterns of the communities across a variety of crop types and compare these with other agricultural systems on a global scale.

9.2 Rove Beetles in the Forests of Canada

Rove beetles are useful as ecological indicators of changes in managed forests because of their high local abundance and diversity and ease of collection (Paquin and Dupérré 2001; Pohl et al. 2008). Often, rove beetles represent a large proportion of the total abundance and richness of organisms collected in pitfall traps, a method commonly used in biomonitoring studies. For example, Klimaszewski et al. (2005, 2007a, 2008a) reported that both abundance and species richness of rove beetles were much greater than those of ground beetles, another taxon commonly used in the evaluation of impacts of forest management, in yellow birch-balsam fir forests in Quebec. In the Quebec study (Klimaszewski et al. 2008a), rove beetles were ca. five times more abundant (9424 specimens) and were ca. three times more diverse (116 species) than ground beetles (Carabidae) (1875 specimens and 38 species). Unfortunately, rove beetle assemblages are often neglected in biomonitoring studies because of the difficulty in identifying species. However, this may change with advances in traditional tools such as taxonomic keys complemented by high-resolution imagery. Examples of recent modern generic and provincial treatments of Canadian Aleocharinae species are as follows: Aleochara (Klimaszewski 1984); *Placusa* (Klimaszewski et al. 2001);

Tinotus (Klimaszewski et al. 2002); Silusa (Klimaszewski et al. 2003); Leptusa (Klimaszewski et al. 2004); Oxypoda (Klimaszewski et al. 2006); Calodera (Assing 2007, 2008); Gnypeta (Klimaszewski et al. 2008b); Diglotta and Halobrecta (Klimaszewski et al. 2008c); Schistoglossa (Klimaszewski et al. 2009a); Gyrophaena and Eumicrota (Klimaszewski et al. 2009b); Alisalia (Klimaszewski et al. 2009c); Dinaraea (Klimaszewski et al. 2013a); Gnathusa, Mniusa and Ocyusa (Klimaszewski et al. 2014); Mocyta (Klimaszewski et al. 2015a); Clusiota and 2007; Atheta (Klimaszewski and Majka Klimaszewski et al. 2015b); Liogluta (Klimaszewski et al. 2016b); Aleocharinae of Nova Scotia (Klimaszewski et al. 2007b; Majka and Klimaszewski 2008a, b, c, 2010; Majka et al. 2008); Aleocharinae of Yukon (Klimaszewski et al. 2008d, 2012); Aleocharinae of Ontario (Brunke et al. 2012); Aleocharinae of Newfoundland and Labrador (Klimaszewski et al. 2011, 2016c); Aleocharinae of New Brunswick (Klimaszewski et al. 2005; Webster et al. 2009, 2012, 2016a, b); and Aleocharinae of Saskatchewan and Alberta (Klimaszewski et al. 2015c, 2016b, d). As a result of the above publications, the number of species reported from Canada increased rapidly with modern diagnostic tools now available for species identification. Despite these advances, the aleocharine tribe Athetini, which includes the large genus Atheta, still remains poorly known, and additional studies across Canada are needed to address present taxonomic and environmental needs.

Advances in DNA barcoding may increase the use of rove beetles in biomonitoring, particularly given the extra time required to dissect and prepare genitalia from specimens to verify species identity. The BOLD (Barcode of Life Data Systems) and GenBank DNA databases of rove beetle species with registered barcodes are constantly expanding. The number of Staphylinidae species in BOLD is currently 2753, with 2104 of those having barcodes. However, clear protocols on genital dissection and preparation are widely available (Hanley and Ashe 2003) and can be followed by non-specialists including beginning students, volunteers or research technicians that may not possess a background in entomology. By following these protocols and newly available taxonomic keys, species-level identifications can often be made with little more effort than what is required for other taxa such as ground beetles (Coleoptera: Carabidae) and spiders (Araneae). With little training, these traditional morphological methods for species identification may still provide a cost-effective means of including rove beetles in biomonitoring.

Rove beetles may provide a higher resolution for forest biomonitoring studies than other commonly used arthropod groups (ground beetles and spiders) because of their strong affinities for specific stand types and the microhabitats that lie within (Pohl et al. 2007, 2008). They occur widely in the forest litter but are often associated with small-scale heterogeneity such as fruiting bodies of fungi and residual deadwood (Klimaszewski et al. 2005). Their seemingly tight relationship with microhabitats and forest structures such as downed wood make rove beetles useful tools for evaluating the effects of forest management. In many cases species can be characterized as forest specialists with strong affinity for intact forest stands (and the microhabitats that lie therein) that have not been recently disturbed by forest management. Species groups that are specific to undisturbed forests are key to assessing forest integrity as we apply a natural disturbance emulation paradigm in our forest management process. These are the species that best tell us how effective we are at preserving forest integrity in managed forests.

Rove beetle assemblages have been used to evaluate impacts on biodiversity of a variety of silvicultural approaches, including small-scale gap cuts that generate within-stand heterogeneity, site preparation of soils for replanting in gaps and larger cuts (Klimaszewski et al. 2008a), removal of residual biomass and overstorey trees in the context of forest biomass removal for bioenergy (Work et al. 2013) and the use of retention patches to emulate larger landscape patterns of fire skips in large harvest blocks (Pohl et al. 2007, 2008). These examples are covered in Sects. 9.4–9.7.

9.3 Diversity of Trophic Relationships and Sensitivity to Changes

Feeding preferences in rove beetles are highly diverse, but initial studies on rove beetle diet preferences are being revised with newer molecular tools. For example, the rove beetle gut microbiota play key roles in the metabolism and health of their hosts. The identification of the fungal taxa that inhabit the gut of rove beetles provides information on the diet of their host and on their potential endosymbionts and on the fungal communities that occupy microhabitats along with rove beetles. The first studies using DNA methods to investigate the gut contents of rove beetles were recently conducted using several abundant species in boreal balsam fir forests of Quebec (Klimaszewski et al. 2013b; Stefani et al. 2016). Nine rove beetle species representing three subfamilies were recently targeted to investigate the fungal diversity present extracts: in gut Atheta strigosula, Atheta terminalis, ventricosa, Liogluta Lypoglossa franclemonti, Atrecus microcephalus, Gabrius brevipennis, Quedius labradorensis labradorensis, (=*fimbriatum*) Ischnosoma longicorne and Tachinus quebecensis (Stefani et al. 2016). In total, we obtained 441 sequences of ITS rDNA representing 42 fungal operational taxonomic units (OTUs) from 9 species of rove beetles (Stefani et al. 2016). OTU richness per beetle species ranged from 4 in Tachinus quebecensis to 16 in Atheta ventricosa. The fungal mycobiota in the posterior gut was dominated by Saccharomycetales (12 OTUs) and Sordariomycetes (9 OTUs), and the core mycobiome of the posterior gut extracts was dominated by 3 OTUs related to yeast, i.e. Candida mesenterica, Debaryomyces spp. and Ophiostoma pluriannulatum (Fig. 9.1). Predominance of yeasts and podocarp fungal spores in the posterior gut of



Fig. 9.1 Fungal OTU richness recorded within nine rove beetle species of three subfamilies of Staphylinidae (upper part of the figure) and relative abundance of the nine fungal classes recorded in the gut contents of the nine

rove beetles suggests that these may play an important role in their dietary requirements and as endosymbionts (Klimaszewski et al. 2013b; Stefani et al. 2016). Particularly, *Sordariomycetes* and some podocarp fungi found in guts have an affiliation with decaying wood. This is an important link to understand interactions between rove beetles, fungi and woody debris and, consequently, how the depletion of woody debris in different forestry practices impacts rove beetles and other organisms

rove beetle species (bottom part of the figure). The A, B and Z upper case letters preceding the fungal class names designate the phyla *Ascomycota*, *Basidiomycota* and *Zygomycota*, respectively (after Stefani et al. 2016)

involved in organic matter decomposition and subsequent nutrient cycling, as well as tree growth.

9.4 The Effects of Small-Scale Gap Cutting

Large-scale, even-aged silvicultural approaches such as clearcutting in Canada are often criticized as unsustainable by the public and by policymakers alike. Large clearcuts can reduce biodiversity through habitat loss if applied widely over forested landscapes primarily by homogenizing the stand structure and eliminating important microhabitats, including deadwood and other ecological legacies (Venier et al. 2014). This has led to wider implementation of alternative silvicultural approaches that create uneven-aged stands and maintain stand heterogeneity, such as partial cutting or gap cutting. Often, uneven-aged silvicultural approaches are inspired by natural disturbances caused by fires of variable intensity, insect outbreaks, windthrow events and even forest gap dynamics.

Small-scale disturbance events, such as gap dynamics, create heterogeneity in light and soil nutrient availability (Paré et al. 1993) and are important in the recruitment of structural features such as downed woody debris (Siitonen 2001). Ultimately, gaps influence future stand composition, typically by maintaining early-successional deciduous species that would otherwise be competitively replaced during succession (Lieffers et al. 1996; Kneeshaw and Bergeron 1998). Stand heterogeneity created by gaps is thought to have additional benefits for biodiversity and generally is more socially acceptable. Changes in the abundance, species richness and community composition of rove beetles were evaluated in response to three configurations of experimental gap cuts and clearcutting in an early-succession yellow birch-dominated boreal forest in Quebec, Canada (Klimaszewski et al. 2008a). In each gap cut, total forest removed was held constant (35% removal by partial cutting with a concomitant decrease in gap size), but the total number of gaps was increased (two gaps, 56 m diameter, 2513 m^2 ; four gaps, 40 m diameter, 1257 m²; and eight gaps, 28 m diameter, 628 m^2) resulting in an experimental increase in the total amount of 'edge' within each stand. In the four- and eightgap treatments, half of the gaps were scarified. In the two-gap treatment, one randomly selected half of each gap was scarified. The scarification was relatively light and affected only surface soil layers. Estimates of species richness using rarefaction were highest in the clearcut and two-gap treatments, decreased in smaller and more

numerous gaps and were significantly higher in scarified areas than in unscarified areas. The total catch of all rove beetles was significantly higher in uncut forests than in the treated areas (Fig. 9.2). Composition of rove beetle assemblages among intermediate- and small-sized gap treatments (four- and eight-gap cuts) was more similar to that in uncut control forests than were those of larger gap treatments (two-gap) and clearcuts (Klimaszewski et al. 2008a). When the total area of forest removed was held constant, smaller, more numerous gaps were more similar to uncut control stands than to larger gaps and fell more closely within the natural forest heterogeneity. The smaller and more numerous gaps were a better emulation of natural stand dynamics than the larger gaps and clearcuts.

9.5 Community Structure and Indicator Species in Gap Cuts

Rove beetle composition responded significantly to increasing gap size. Composition among intermediate- and small-sized gap treatments (fourand eight-gap treatments) was more similar to that of uncut control forests than were those of larger gap treatments (two-gap) and clearcuts. Differences in rove beetle assemblage (defined primarily by a loss of closed-canopy species and an increase in species with an affinity for open habitats) relative to control plots were more pronounced in two-gap treatments and clearcuts than in four- and eight-gap treatments. These assemblage differences were made greater by scarification. Assemblages of rove beetles were less affected by numerous small gaps with increased edge relative to fewer larger gaps with less edge. It may be that the smaller gaps (28 m in diameter) were perceived by forest specialists as an extreme case of stand heterogeneity rather than perceptible gaps as rove beetles were much more abundant there than in larger gaps (Klimaszewski et al. 2008a). Smaller gaps may also be considered more permeable for dispersion than larger gaps.



Fig. 9.2 Standardized catch (mean +/- standard error) of total rove beetles, forest specialists, forest generalists, hygrophilous species and open-habitat specialist in

controls and each harvesting and scarification treatment (after Klimaszewski et al. 2008a)

Of the 116 species represented, 6 species dominated the total catch: Tachinus fumipennis (Say) (55.4% of the total catch), Oxypoda convergens Casey (10.6%), Atheta pseudo-Klimaszewski Placusa modesta (6.6%),tachyporoides (Waltl) (3.7%),Tachinus addendus Horn (3.5%) and Bisnius blandus (Gravenhorst) (2.5%) (Klimaszewski et al. 2008a). Together these species represented over 82% of the overall catch, but there were 27 additional significant indicator species associated with different treatment as illustrated in Fig. 9.3.

9.6 Effects of Scarification in Gap Cuts

Scarification of forest soils is used to expose mineral soils and promote seed germination of particular species (Prévost et al. 2009). In the experimental gap cuts described above, an additional scarification treatment was applied, and responses of rove beetle assemblages were compared between scarified and non-scarified gap cuts (Klimaszewski et al. 2008a). In yellow birch-dominated forests, scarification is done to promote germination of yellow birch and red spruce trees. In scarified plots, rove beetle richness was greater than in non-scarified plots. Initially, this result seemed counter-intuitive, because we thought that homogenization of microsites by scarification would reduce species richness. However, when applied to small gaps, scarification may actually increase overall habitat heterogeneity at the stand level by creating recently disturbed soils in close proximity to intact closed-canopy forest. Scarification also altered overall composition of rove beetles through an interaction with gap size. Scarification effectively nullified any compositional differences attributed to larger gaps, thus making large, scarified gaps indistinguishable from clearcuts (Klimaszewski et al. 2008a). In smaller gaps, scarification acted as secondary, compounding



Fig. 9.3 Differences in mean catch rate of significant indicator species: (a) clearcut and two-gap treatments (n = 16), (b) four- and eight-gap scarified treatments

disturbance event to alter composition between scarified and unscarified small gaps (Klimaszewski et al. 2008a).

9.7 Effects of Biomass Removal

Increasing interest in harvesting biomass for energy and non-timber forest products stems from the need to offset the decline in markets for traditional wood products and to mitigate climate change. While the development of bioenergy has

(n = 8), (c) four- and eight-gap unscarified treatments (n = 8) and (d) uncut control stands (n = 4) (after Klimaszewski et al. 2008a)

potential for economic, social and environmental benefits, there remains concern about the impact of biomass harvesting on the long-term sustainability of the forest and the long-term sustainability of biodiversity. While wood residues from forest harvesting or salvaged wood from insect outbreaks or forest fires are considered as biomass 'feedstocks' for bioenergy production, they also provide reserves of nutrients and moisture, microsites and substrates for seedlings and habitat and resources for other organisms such as arthropods, bacteria and fungi. These attributes of woody debris play major roles in ecosystem functioning and in sustaining biodiversity (Stockland et al. 2012). Two studies using rove beetles were recently conducted to evaluate the impacts of different intensities of postharvest slash removal on rove beetle abundance, species richness and community composition, one in jack pine forest of the Island Lake Biomass Harvest Research and Demonstration Area, also known as Island Lake Site (ILS), in Ontario (Venier et al. 2017; Work et al. in preparation), and the other in a balsam fir-white birch forest at the Montmorency Teaching and Research Forest (MTRF), Quebec (Work et al. 2013; Klimaszewski et al. unpublished). The ILS evaluated changes in species composition of litter-dwelling arthropod taxa, including rove beetles, in response to a gradient of forest disturbance including the following treatments, from the least to the most disturbed: 85-year-old postfire forest (old control), 45-year-old postharvest plantation forest (young control), 3-year postfire treatment (fire control), 3-year post stem-only harvesting (SOH) with branches and tops left at the stump, 3-year post whole-tree biomass harvesting treatment (WTH) with branches and tops moved to roadside, 3-year post WTH with stumps removed and 3-year post WTH with forest floor removed by blading (Venier et al. 2017).

When rove beetle assemblages were compared between uncut stands and harvested stands with increasing removal of biomass, composition was markedly different between older uncut stands (85 years) and all other treatments, including the 45-year-old closed-canopy control. The vast majority of species and individuals were associated with the old-forest treatment, whereas very few individuals were captured in the other treatments. For example, of the 1231 individuals captured, 745 were captured in the five 85-yearold control plots, whereas only 486 were captured in the other 30 plots of all other treatments combined. Species strongly associated with older, uncut forest included Atheta capsularis, Atheta strigosula, Lordithon fungicola, Oxypoda grandipennis, Atheta remulsa and Aleochara fumata (occurred also in harvested sites) and were found only in very small numbers or not at all in harvested, fire disturbed and young control treatments. Only two species were associated with the harvested sites or younger stands, i.e. Aleochara fumata and Mycetoporus consors (Venier et al. 2017). Atheta capsularis, A. strigosula, L. fungicola and O. grandipennis are generally associated with forest litter, while Aleochara fumata is a more opportunistic and mobile species. Its life history depends on the availability of habitats with dipteran larvae and pupae, which are more randomly distributed in the forest. Moist litter is a very important habitat for the majority of rove beetles because their small bodies are prone to desiccation. Removal of the litter layer and exposure of mineral soil likely reduce soil moisture and habitat suitability for rove beetles. Among the harvested treatments, rove beetle composition did not differ between tree-length and full-tree harvesting. This could result from the presence of only a few generalist or accidental species and lack of true microhabitat specialists.

Lack of canopy and extensive biomass removal, including the removal of soil organic layers by blading, had strong effects on rove beetles. This treatment dramatically removed much of the habitat where a majority of rove beetles live. Removing the whole organic layer and deadwood from postharvest plots eliminates the buffer zone protecting subsequent layers of ground habitat from reduced humidity and increased temperature.

Interestingly, however, rove beetles responded similarly to other litter-dwelling taxa (ground beetles and spiders) to the gradient of disturbance across the other treatments. This response suggests that litter-dwelling communities respond strongly to forest floor disturbance and canopy cover and that harvesting does not effectively mimic fire disturbance (Venier et al. 2017), at least in this instance. These results also indicate that ground-dwelling arthropod communities are not differentially affected by full-tree harvesting and tree-length harvesting, but they are more sensitive to extreme levels of biomass removal such as stump removal and forest floor removal (Venier et al. 2017). Rove beetles in jack pine forests may serve as good indicators of mature forest conditions but are likely less effective as indicators of biomass removal due to their relatively low numbers in harvested plots (Venier et al. 2017). This illustrates that jack pine forest is different from broadleaved, mixed and other coniferous forests as habitat for rove beetles. It is a drier, more open forest with less ground floor litter, while the others, particularly broadleaved and mixed forests, provide a richer and moister ground litter, which is a more suitable habitat for these beetles.

In the 2011 MRTF study, changes in rove beetle abundance and assemblages were compared between two treatments and a control: clearcuts where branches and non-merchantable portions of the stem were left on site (stem-only harvesting or SOH); whole-tree harvesting (WTH), in which stems, tops and branches are removed; and uncut control plots (C) in about 42to 60-year-old mature balsam fir stands in Quebec (Work et al. 2013). Overall catch rates were much greater in uncut plots (C) than in either SOH or WTH sites. The high overall abundance and differences in assemblage composition in uncut stands are attributable mainly to the presof Atheta capsularis, ence Α. klagesi, A. strigosula and Tachinus fumipennis/frigidus in controls. Among the clearcuts, catch rates in WTH were greater than in SOH sites, where three species (like Pseudopsis subulata, Quedius labradorensis and, to a lesser extent, Gabrius brevipennis) were more abundant when branches and finer woody debris had been removed. These differences between SOH and WTO in balsam fir-dominated stands contrast with the response of rove beetles in jack pine stands at the ILS experiment, where no differences in rove beetles were observed.

In 2013 (3-year post-clearcut), rove beetles were resampled at the MRTF experiment, with an inclusion of the additional treatment (ADR), in which all woody debris were removed from new clearcut plots and samples were also taken from different chronosequences of the surrounding forests (11-, 22-, 42- and 73-yearold stands) (Klimaszewski et al. in preparation). We collected 2069 specimens and 87 species of Staphylinidae in 10 subfamilies in harvesting

treatments and 5291 specimens and 86 species in 12 subfamilies in chronosequence stands. The oldest chronosequence stand (73 years) had a distinct rove beetle community, and the communities in the younger chronosequence stands (11, 22, and 42 years) and in the control (C) stand were similar to each other and distinct from the harvesting treatments. Rove beetle abundance showed little relation to differences in fine or coarse woody material. However, staphylinid species richness was positively affected by higher fine woody debris volume. In this 3-year post-clearcut resampling, Atheta capsularis, A. klagesi, A. ventricosa, Liogluta terminalis (=L. aloconotoides), Lypoglossa franclemonti, Placusa tachyporoides, Acidota quadrata, Proteinus sp., Quedius rusticus, Q. densiventris and Tachinus species (mainly T. frigidus and T. fumipennis) showed strong affinities for uncut forests, whereas several other species were more or equally abundant in treatments: Gabrius picipennis (SOH, ADR, WTH), G. brevipennis (SOH, WTH, ADR), Quedius labradorensis (SOH, ADR, WTH), Q. peregrinus (WTH, SOH, ADR), Ischnosoma longicorne (SOH, ADR, WTH), I. splendidum (SOH, ADR, WTH), Parascydmus corpusculus (SOH, WTH, ADR) and Pseudopsis subulata (WTH, SOH, ADR). Harvesting and biomass removal significantly reduced the mean abundance of several species of rove beetles in the subfamilies Aleocharinae, Omaliinae and Tachyporinae and increased or maintained the mean abundance of predatory species of subfamilies Staphylininae and Scydmaeninae, compared with uncut control plots. The species from the latter two subfamilies may find more diverse prey species in harvested forests. However, overall catch of rove beetles was not significantly affected by harvesting treatment, likely because the abundance of tolerant and openhabitat species such as Ischnosoma longicorne, Gabrius brevipennis, Pseudopsis subulata and Parascydmus corpusculus increased and compensated for the decreased abundance of forest specialists such as Atheta capsularis, A. klagesi and Tachinus frigidus in harvested plots. Many species in the subfamilies Aleocharinae, Omaliinae and Tachyporinae are dependent on wet litter, fungi and specific microhabitats that are more frequently found in mature closed-canopy forests than in open, recently harvested forests. These forest species require closed-canopy forests such as those found in control and chronosequence forest plots, less light, more humidity, moist litter including woody debris, specific species of fungi (associated with woody debris) and arthropod prey species that also prefer closed-canopy forests and associated microhabitats, such as under the bark of moist logs (e.g. Placusa species) or wet moss (e.g. Acidota quadrata) (Campbell 1982; Klimaszewski et al. 2001). Many rove beetles are associated with fungi (Newton 1984), and analyses of the gut contents of several forest specialists (e.g. Atheta capsularis, A. klagesi, Tachinus frigidus, T. fumipennis) revealed the presence of budding yeasts and podocarp spores of different fungi (Klimaszewski et al. 2013b). The reduced abundance of some forest specialists in harvested treatments may be due, in part, to the reduced abundance of fungi with which they are associated. Ischnosoma longicorne was captured in comparable numbers in SOH plots as in the uncut controls, but in lower numbers in WTH plots, suggesting that this species may be best suited to intermediate deadwood conditions. Gabrius picipennis is a common species occurring in a wide range of habitats and is the only species of Gabrius that exhibits a remarkable variability in almost all external morphological characters (Smetana 1995). Placusa tachyporoides is a subcortical species, and clearcut diminishes its preferred habitats, i.e. standing trees and logs (Klimaszewski et al. 2001). Again, details of habitat preferences of Liogluta terminalis remain elusive (Lohse et al. 1990, Work et al. 2013, as L. aloconotoides). Harvesting treatments significantly affected rove beetle species richness (Fig. 9.4), but not species evenness. This indicates that a majority of the rove beetle species studied were forest litter species and their occurrence in treated plots was significantly affected by environmental conditions changed by harvesting, including the



Fig. 9.4 Rove beetle species richness in the Montmorency Teaching and Research Forest, Quebec, that was subjected to different silvicultural treatments (2013): CO, untreated controls; SOH, stem-only harvesting; WTH, whole-tree harvesting; and ADR, all debris removed. The effect of harvesting intensity treatment on mean total season catch per plot of Staphylinidae (all species

pooled), and individual species for which more than ten specimens were collected, was tested by one-way ANOVA and the Tukey post hoc test in SAS PROC GLM (SAS Institute 2002–2003). We report mean (\pm SE) catches per 100 trap days per plot of non-transformed data

amount of deadwoody debris and exposure to light. Light conditions for beetles improved within 3 years of harvesting in comparison with immediate postharvesting conditions in harvesting treatment plots because of fastdeveloping vegetation that increased the cover. Mean catches of several abundant forest specialist species were significantly greater in control stands than in the harvest treatments, and these species may be considered indicators of uncut forests and may thus be used to determine when regenerating sites have moved on to forested conditions.

9.8 Responses to Large-Scale Fire Events

Fire is the dominant disturbance in the Nearctic boreal forest (Pohl et al. 2008). It has a profound effect on rove beetles by destroying forest communities to an extent that depends on fire intensity and by resetting the successional trajectory to its earliest stages (Pohl et al. 2008). The burn pattern results in a patchwork of different communities at various stages in the successional cycle. In contrast to fire, forest harvesting does not directly destroy the rove beetle community, but to a large extent, it destroys the forest habitat (Pohl et al. 2008). This results in a unique rove beetle community characterized by a mix of forest species and open-ground specialists and overall high diversity in this period of flux (Pohl et al. 2008). In the years following harvesting, the rove beetle community goes through successional changes and becomes more similar to the mature forest community, but it skips the early postfire stage and proceeds along the successional trajectory more rapidly than after fire (Pohl et al. 2008). Other less direct effects of harvesting on rove beetles are a decrease in the proportion of landbase suitable for communities associated with older successional stages, alteration of forests by postharvest site preparations and planting of exotic tree species, edge and fragmentation effects that are detrimental to the remaining forest surrounding harvested areas and an influx of exotic arthropod species with affinities for

disturbed sites (Pohl et al. 2008). It is recommended that future work explore the effects of postharvest forestry activities, fragmentation, edges and changes in riparian zones and wetlands on rove beetles in forested habitats (Pohl et al. 2008).

9.9 Rove Beetle Biological Control Services in Canada

In addition to being important components of nutrient cycling communities in the world's forests, rove beetles are abundant in anthropogenic habitats such as agroecosystems. Predatory or omnivorous species in these communities are known to provide biocontrol services to agriculture by suppressing pest populations, usually as generalists or occasionally as specialists, of diverse arthropods such as spider mites (Kishimoto and Adachi 2008), cereal aphids (Dennis and Wratten 1991), horn flies (Hu and Frank 1995), wireworms (Fox and MacLellan 1956) and cabbage maggots (Andreassen et al. 2010). Biocontrol services by rove beetles in Canadian agroecosystems are rarely documented and little understood, likely due to a long history of inadequate taxonomic knowledge that made identifications difficult or impossible, a situation that has only recently improved (see references in Sect. 9.1). This important first step forward has made detailed, species-level surveys more tractable, and rove beetle communities may soon become accessible to agroecologists as taxonomic knowledge and associated identification resources continue to improve.

9.10 Rove Beetle Assemblages in Canada's Diverse Agroecosystems

In Canada, rove beetle assemblages in soybean and blueberry fields and in dairy pastures have been surveyed in detail (D'Orsay 2012; Renkema et al. 2012; Brunke et al. 2014); nearby, those of vegetable crops have been sampled in Pennsylvania, USA (Leslie et al. 2007). Conducted prior to the recent advances made in the taxonomy of the Aleocharinae, the most diverse and difficult subfamily of Staphylinidae in Canada, a detailed survey in Canadian raspberry fields necessarily omitted this group from their study. However, the results obtained by Levesque and Levesque (1996), who used multiple trap types, are noteworthy among North American studies for including detailed phenological information such as flight activity period and field colonization. Staphylinid assemblages in agroecosystems of northeastern North America contain high percentages of adventive species: 58.3% in dairy pastures, 43.1% in soybean fields, 39.6% in blueberry fields and 33% overall in diverse vegetable crops (Leslie et al. 2007; D'Orsay 2012; Renkema et al. 2012; Brunke et al. 2014). For most of these assemblages, more than half of the common species ($\geq 1\%$ of total individuals) (Table 9.1) were adventive: 71.4% in dairy pastures, 57.1% in soybean fields, 58.8 in blueberry fields and 33% in diverse vegetable crops. However, native species may still contribute positively to biocontrol as the most abundant species captured in Canadian were Strigota obscurata agroecosystems Klimaszewski and Brunke, Stenus erythropus (Melsheimer) and Stenus flavicornis Erichson (Table 9.1), native rove beetles that favour open habitats. Several staphylinids were shared between northeastern assemblages, which indicate that although agroecosystems differ strongly in physical structure and management their practices, some species may be broadly tolerant to the challenges presented by frequent disturbances and unpredictable prey populations (Wiedenmann and Smith 1997). Generally, these species tend to be ubiquitous or prefer earlysuccession natural or disturbed habitats (Andersen 1991; Brunke et al. 2014). The most widespread common species across agricultural habitats were Amischa analis (Gravenhorst), Dinaraea angustula (Gyllenhal) and Strigota ambigua (Erichson), all Aleocharinae. Relatively few of the 34 staphylinid subfamilies are major elements in the fauna of Canadian agroecosystems, and common species are generally limited to seven subfamilies: Aleocharinae, Omaliinae, Oxytelinae, Paederinae, Staphylininae, Steninae and Tachyporinae.

9.11 Temporal and Spatial Dynamics

Staphylinids in Canadian agroecosystems are typically univoltine, with two peaks in activity each year: one after overwintering or summer aestivation and one after the eclosion of the next generation (Boiteau 1983; Levesque and Levesque 1996; Brunke et al. 2014). The majority of common species in those studies were most active between May and July and exhibited a decline in surface/flight activity as the growing season progressed. Late summer inactivity at the soil surface is typical of adult staphylinids in agroecosystems, though some Aleocharinae have been observed to maintain activity throughout the growing season (Levesque and Levesque 1996). Little is known about the activity of both adult and larval staphylinids below the soil surface. Exceptions to this pattern are known in the Tachyporinae and Omaliinae, which contain species such as Tachinus corticinus Gravenhorst and Arpedium cribratum Fauvel that prefer cooler temperatures and can be important members of an agroecosystem assemblage early or late in the season when many other staphylinids are less abundant (Levesque and Levesque 1996; Brunke et al. 2014). Staphylinid dispersal into Canadian agroecosystems by flight is known to occur predominantly in late spring/early summer (Boiteau 1983; Levesque and Levesque 1996). Dispersal of rove beetles into the interior of Canadian soybean fields does not appear to be challenging for common species of the assemblage, likely due to high dispersal power via flight (Brunke 2011). However, fewer staphylinids (mostly Philonthus spp., all flight-capable) were captured in the centre of potato fields in New Brunswick (Boiteau 1983) and may have preferred the more densely vegetated microhabitats of the field and woodland edges. A few species with low flight activity among individuals (e.g. Neohypnus spp., Xantholinini) or with small proportions of fully **Table 9.1** Common species of Staphylinidae ($\geq 1\%$ of total species captured in pitfall traps) in northeastern North American agroecosystems ranked from highest to lowest activity density. Rankings for vegetable crops were estimated from bar graphs in Leslie et al. (2007). Species occurring in three or more agroecosystems are in boldface, while other shared species are underlined. Adventive species are indicated by '+'. Modified from Brunke et al. (2014)

	Vegetable field crops		Dairy pastures (Nova
Soybean (Ontario) ^a	(Pennsylvania) ^b	Blueberries (Nova Scotia) ^c	Scotia) ^d
Strigota	Dinaraea angustula	Stenus erythropus	Stenus flavicornis
obscurata Klimaszewski and	(Gyllenhal) ⁺	Melsheimer	Erichson
Brunke		TV 1 1' 1' '	G
Apocellus sphaericollis (say)	Hoplandria lateralis	Xantholinus linearis	Stenus erythropus
	(Weisneimer)	(Olivier)	D1:1 dl l i
(Fabricius) ⁺	Strigota ambigua (Frichson)	$\frac{MOCYIA JUNGI}{(Gravenborst)^+}$	(Gravenhorst) ⁺
Dingrang groustulg	Tachyporus nitidulus	Drusilla canaliculata	Philorthus cognetus
(Gyllenhal) ⁺	(Fabricius)	$\frac{Drustita}{(Fabricius)^+}$	Stephens ⁺
Hoplandria lateralis	Anotylus spp	Philonthus carbonarius	Tachyporus dispar
(Melsheimer)	moryno spp.	(Gravenhorst) ⁺	(Paykull) ⁺
Aleochara verna Sav	Aleochara verna sav	Octhephilium fracticorne	Philonthus varians
	<u> </u>	(Paykull) ⁺	(Paykull) ⁺
Strigota ambigua (Erichson)	Neohypnus spp.	Stenus semicolon LeConte	Tachinus rufipes
			(DeGeer) ⁺
Oxypoda brachyptera	Tachinus fimbriatus	Anotylus rugosus	Rugilus angustatus
(Stephens) ⁺	Gravenhorst	(Fabricius) ⁺	(Geoffrey) ⁺
Anotylus tetracarinatus	Aleochara curtula	Gabrius picipennis	Amischa analis
(block) ⁺	(Gravenhorst) ⁺	(Mäklin)	(Gravenhorst) ⁺
Anotylus insecatus (Erichson) ⁺	Belonuchus rufipennis (Fabricius)	Oxypoda nigriceps Casey	Tachinus addendus horn
Amischa spp. ^e	Gabrius nigritulus	Dinaraea angustula	Gabrius picipennis
	(Gravenhorst) ⁺	(Gyllenhal) ⁺	(Mäklin)
Anotylus rugosus (Fabricius) ⁺		Mycetoporus horni	<u>Mocyta fungi</u>
		Berhauer & Schubert	(Gravenhorst) ⁺
Stethusa spuriella (Casey)		Amischa analis (Gravenhorst) ⁺	Lathrobium spp.
Scopaeus minutus Erichson+		Ilyobates bennetti	Aleochara morion
		Donisthorpe ⁺	Gravenhorst ⁺
Tachinus corticinus		Mycetoporus consors	Gyrohypnus angustatus
Gravenhorst ⁺		LeConte	(Stephens) ⁺
		Strigota ambigua	
		Quadius curtinannis	
		Bernhauer ⁺	

^aBrunke et al. (2014); ^bLeslie et al. (2007); ^cRenkema et al. (2012); ^dD'Orsay (2012)

^eIncluded at least some individuals of Amischa analis

winged individuals (e.g. *Arpedium cribratum*) disperse from source populations primarily over the soil surface (Levesque and Levesque 1996) and may exhibit patchier local distributions. Overwintering may occur within fields in some species, but many are thought to disperse to nearby hedgerows or forest edges, which are known to support agriculturally significant

staphylinids outside of the growing season (Holland et al. 2009; Brunke et al. 2014). Based on both passive (traps placed in crop vegetation) and active (sweeping, suction) sampling, some staphylinids are known to spend a considerable percentage or most of their active time in agroecosystems above the soil surface (Brunke 2011; D'Orsay 2012), potentially preying upon foliar pests such as aphids, caterpillars or the eggs of various taxa; Canadian species with high levels of foliar activity include *Amischa analis, Anotylus tetracarinatus, Mocyta fungi, Stenus flavicornis* and *Tachyporus dispar* Paykull.

9.12 Conservation Biological Control by the Generalist Predator Assemblage

Staphylinids are abundant and widespread members of the diverse predator assemblages that occur in Canada's agroecosystems, and as such they have been targeted under 'conservation biocontrol' efforts, which aim to promote these assemblages through crop management techniques (Symondson et al. 2002). Such techniques, of which the impact on staphylinids has been investigated, include the provision of hedgerows or non-crop buffers, mulching and reduced weeding. In Europe, hedgerows provide staphylinids with overwintering habitat and refugia from disturbances during the growing season (Holland et al. 2009). The direct impact of non-crop buffers has not been investigated in Canada, but they are known to support important staphylinids of the soybean assemblage outside of the growing season (Brunke et al. 2014). Mulching in highbush blueberry, a management practice used to deter successful pupation in the blueberry maggot (Renkema et al. 2011), was observed to increase the abundance of rove beetles in Nova Scotia, Canada; species responded differently depending on whether compost or pine needles were applied (Renkema et al. 2012). Positive effects on the diversity and abundance of some species increased the following year, suggesting that the mulched areas were creating local, stable increases in available prey or preferred microclimates (Renkema et al. 2016). Non-weeded areas promoted the abundance of several staphylinids, including Xantholinus linearis (Olivier), Anotylus rugosus (F.), Mocyta fungi and Gabrius picipennis (Mäklin) (Renkema et al. 2012).

One of the greatest challenges to successful conservation biological control is the complex

network of interactions between predator and potential prey and between individual predator species. For example, intraguild predation by the large carabid Pterostichus melanarius Illiger of smaller predator beetles, including staphylinids, suppressed the predation of pest *Delia* (Diptera) eggs by the small beetles (Prasad and Snyder 2004). This negative interaction may be improved by creating refugia for smaller predators such as those provided by weed cover (Prasad and Snyder 2004). Even more remarkable are intraguild interactions that have a positive impact on biological control services. In Mexican shaded coffee plantations, the aleocharine Myrmedonota xipe Mathis and Eldredge recognizes ant alarm pheromones to selectively prey upon phorid fly-parasitized Azteca ants, which are important predators of coffee-feeding insects (Mathis and Tsutsui 2016). It is unknown to which magnitude the staphylinids reduce parasitoid pressure on the ants, but this recent discovery emphasizes the fact that agroecology of conservation biological control is complex and that the poorly known natural history of most insects may be an impedpractical iment to its and predictable implementation.

We propose that the agroecological study of staphylinids faces an even greater issue: the basic diet of most rove beetle species is unknown, and much of what is stated in the literature is based on assumptions. Often, species are considered mycophagous or saprophagous based on observations of species of the same genus or subfamily. This is less problematic for the entirely predaceous and agriculturally important subfamilies Paederinae, Staphylininae and Steninae (Thayer 2005), but diet is complex and variable within the equally important subfamilies Omaliinae, Aleocharinae, Oxytelinae and Tachyporinae. For example, Tachyporus dispar (Tachyporinae), an important aphid predator in Europe, also feeds on the powdery mildew growing on the exudate produced by cereal aphids (Dennis et al. 1990). The diverse and widespread genus Sepedophilus (Tachyporinae) is often treated as uniformly mycophagous (Levesque and Levesque 1995; Clough et al. 2007;

Renkema et al. 2012), but a study based on gut contents and mouthpart morphology (Newton 1984) revealed that the species found in Nearctic and Palearctic agroecosystems (i.e. S. marshami and S. testaceus) belong to a predatory group with potential facultative mycophagy ('Group A'). Nearly every surveyed agroecosystem contains several species of Anotylus (Oxytelinae), which are normally considered to be entirely saprophagous in dung, compost or carrion (Hammond 1976; Clough et al. 2007; Renkema et al. 2016). However, observations by Horion (1967) and later in the field by Majka and Klimaszewski (2008b) confirm larval Diptera predation by Anotylus insecatus, a Palaearctic species that is adventive in North America (Campbell and Tomlin 1983). A closely related species of similar morphology, Anotylus rugosus, was observed to aggregate near oviposition sites of the cabbage root maggot (Guseva and Koval 2005). A recent study comparing conventional and organic agriculture in Europe found that organic fields contained more 'decomposers' (=saprophages, mostly Anotylus species), while conventional fields contained more predators (Clough et al. 2007). The higher organic content of organic fields was considered to support more decomposers, but it would also support higher prey populations for obligate or facultative predators. A better understanding of predation in common, agriculturally relevant oxyteline and tachyporine species would improve the foundation of studies seeking to reveal differences in responses to crop management among functional trophic groups.

9.13 Biocontrol Services in Simplified Systems

Far more is known about the biocontrol services of staphylinids in simplified systems such as those of the commercially reared *Dalotia coriaria* used in greenhouse integrated pest management and the Diptera predator/parasitoid genus *Aleochara*. *Dalotia coriaria* is a widespread Palaearctic species that has become adventive in the Nearctic and several other regions (Klimaszewski et al. 2013c); it is such a prolific predator of eggs and immatures that it can become a pest of laboratory insect colonies (Miller and Williams 1983). Easily reared on oatmeal but preferring living prey (Birken and Cloyd 2007), *D. coriaria* can be released in greenhouses as part of an integrated pest management strategy against fungus gnats, which are pests of potted plants (Jandricic et al. 2006). Mutual intraguild predation between released staphylinids and predatory mites is known to occur, but future research is needed to determine whether this impacts the overall suppression of greenhouse fungus gnat populations (Jandricic et al. 2006).

The staphylinid taxon that has been given the greatest amount of agroecological research attention is the diverse and widespread genus Aleochara due to the close association of its members with pest Diptera as predators and parasitoids. In the Northern Hemisphere, A. bipustulata (L.), A. bilineata Gyllenhal and A. verna Say (all subgenus Coprochara) are particularly well-studied as natural enemies of root maggots (Delia spp.), which are severe economic pests of canola and cause 20 to 100 million dollars of damage annually in Canada alone (Holliday et al. 2013). These species possess a specialized life cycle, with active, first-instar larvae that seek out cyclorrhapheous fly puparia (Klimaszewski 1984) and enter via a chewed hole, where they feed as ectoparasitoids of the pupae (Colhoun 1953). First-instar larvae overwinter in the puparia (Colhoun 1953). Secondand third-instar larvae are morphologically specialized for sedentary life as ectoparasitoids, and third-instar larvae pupate within their puparium (Colhoun 1953). Both A. verna and A. bilineata occur in the Canadian canola assemblage, but only the latter occurs consistently and emerges in synchronization with the oviposition period of its Delia hosts (Broatch et al. 2008). In Canadian canola, A. bilineata is the most prevalent parasitoid of Delia radicum (L.) due to competition with Trybliographa rapae (Westwood) (Hymenoptera, Figitidae), whose populations experience mortality if larvae of the former attack pupae that were already parasitized by the latter (Hemachandra et al. 2007). Although *A. bipustulata* does not occur in the Nearctic (Hemachandra et al. 2005), there is interest to introduce it intentionally into Canada as a natural enemy of root maggots in canola (Hemachandra et al. 2007). Further manipulation of *Aleochara* biological control services in canola may be made possible by gaining a better understanding of their host location mechanisms, which appear to be based on volatiles released by damaged canola plants (Broatch et al. 2010). An application of mustard seed meal can locally increase the number of adult *A. bilineata* (Holliday et al. 2011) and, potentially, parasitism and predation rates.

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