

Factors influencing dispersal by flight in bark beetles (Coleoptera: Curculionidae: Scolytinae): from genes to landscapes¹

Kelsey L. Jones, Victor A. Shegelski, Nathan G. Marculis, Asha N. Wijerathna, and Maya L. Evenden

Abstract: Dispersal by flight is obligatory for bark beetles in the subfamily Scolytinae. Adult bark beetles must leave the natal host and fly to seek new hosts for brood production. Because of the eruptive nature of some bark beetle populations, dispersal capacity has implications for beetle spread and invasion across the landscape. Bark beetle dispersal can occur over short distances within a stand or over long distances above the forest canopy, where wind aids dispersal. Despite the obvious importance of dispersal for predicting population spread, knowledge gaps in understanding factors that influence bark beetle dispersal remain. In this review, we synthesize information on bark beetle flight to gain a better understanding of this important life history trait. We assess the impact of genetic, physiological, and morphological traits on flight in different bark beetle species. We also consider the impact of abiotic and biotic environmental conditions on flight. We discuss how measurements of these factors could contribute to the development of comprehensive models to better predict spread of bark beetle populations. Through the synthesis of flight research on a variety of bark beetle species, this review provides suggestions for future avenues of research on this important aspect of bark beetle ecology.

Key words: Scolytinae, flight, dispersal, bark beetle.

Résumé : Le vol est le moyen de dispersion obligatoire chez les scolytes dans la sous-famille des Scolytinae. Les scolytes adultes doivent quitter l'hôte où ils sont nés et s'envoler pour chercher de nouveaux hôtes afin d'assurer leur progéniture. À cause de la nature éruptive de certaines populations de scolytes, la capacité de dispersion a des répercussions sur la propagation et l'invasion de l'insecte dans le paysage. La dispersion des scolytes peut survenir sur de courtes distances à l'intérieur d'un peuplement d'arbres ou sur de longues distances au-dessus du couvert forestier où le vent favorise la dispersion. Malgré l'importance évidente de la dispersion pour prédire la propagation de la population, il y a encore des lacunes dans les connaissances concernant la compréhension des facteurs qui influencent la dispersion des scolytes. Dans cette revue de littérature, nous résumons l'information sur le vol des scolytes pour avoir une meilleure compréhension de cet aspect important du cycle vital. Nous évaluons l'impact des traits génétiques, physiologiques et morphologiques sur le vol chez les différentes espèces de scolytes. Nous discutons de la façon dont la mesure de ces facteurs abiotiques et biotiques pourrait contribuer au développement de modèles complets pour mieux prédire la propagation des populations de scolytes. Par le biais de la synthèse de la recherche sur le vol chez une variété d'espèces de scolytes, cette revue de littérature fournit des suggestions pour de futures avenues de recherche sur cet aspect important de l'écologie des scolytes. [Traduit par la Rédaction]

Mots-clés : Scolytinae, vol, dispersion, scolytes.

1. Introduction

Bark beetles, *sensu stricto*, breed and spend most of their life underneath the bark of the host tree. Adult beetles eventually leave the natal host to search for new hosts for brood production. A dispersal phase is obligatory for all bark beetle species but does not necessarily occur in each generation if recolonization of the same host occurs (Raffa et al. 2015). Beetles need to disperse as the resources provided by the natal host become depleted (Raffa et al. 2015). Upon emergence, many beetles initiate flight dispersal downwind until an attractive semiochemical signal is encountered, and then oriented flight upwind occurs in response to the signal (Gray et al. 1972; Safranyik et al. 1992).

Reproductive and life history strategies vary among different species of bark beetle, which can influence dispersal and host

colonization behaviours. In monogamous bark beetle species, best studied in the genus *Dendroctonus*, the female is the pioneer and locates a suitable host before recruiting male beetles for mating and host colonization. In polygamous species, best studied in the genus *Ips*, male beetles pioneer and initiate galleries in the host tree. Females are recruited after the initial host attack. Both monogamous and polygamous bark beetle species attract conspecifics through the use of aggregation pheromones (Raffa et al. 2015). Pioneer beetles release aggregation pheromones after initial feeding to promote conspecific attraction and mass attack of the host tree (Gitau et al. 2013). Beetles of both sexes respond to aggregation pheromones. Individuals of the same sex as the pioneer will land and initiate new attacks on the tree, while beetles of the opposite sex will enter a previously formed gallery to mate

Received 6 July 2018. Accepted 26 March 2019.

K.L. Jones, V.A. Shegelski, A.N. Wijerathna, and M.L. Evenden. Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada. **N.G. Marculis.** Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, Alberta, Canada.

Corresponding author: Kelsey Jones (email: kljones1@ualberta.ca).

¹This review is part of a collection of papers developed through the NSERC-supported Strategic Network Grant "TRIA-Net". TRIA-Net's goal was to apply modern genomic and genetic approaches to improve our understanding of mountain pine beetle outbreaks and to provide tools to forest managers to reduce outbreak risk.

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Table 1. The flight distances and velocities as reported from the literature of bark beetle species.

Species	Method	Distance (km)	Velocity (km·h ⁻¹)	Citation
<i>Dendroctonus ponderosae</i>	Flight mill	2.12–5.95 (mean) 0–24 (total range)	1.55–1.93	Evenden et al. 2014
<i>Dendroctonus armandi</i>	Flight mill	0–48 (total range 1st generation) 0–22 (total range 2nd generation)	2.38 (median)	Chen et al. 2010
<i>Ips sexdentatus</i>	Flight mill Mark–recapture	3–48 (total range) 0–4 (limited by trap distance)	2.9–6.5	Jactel and Gaillard 1991 Jactel 1991
<i>Dendroctonus valens</i>	Mark–recapture	0.55 (mean)		Costa et al. 2013
<i>Dendroctonus pseudotsugae</i>	Flight mill	4.6–32 (total range) 4.2–5.1 (mean)	2.88–5.28 (total range) 1.22–1.36 (mean)	Atkins 1960 Williams and Robertson 2008
	Free flight		3–9 (total range)	Atkins 1960
<i>Dendroctonus frontalis</i>	Flight mill	0.98 (mean) 0.3–2.6 (total range) 2.71 (male mean) 3.37 (female mean)	0.43–1.18 (total range) 1.13 (male mean) 1.16 (female mean)	Kinn 1986 Kinn et al. 1994
<i>Ips typographus</i>	Flight mill	<0.5 (for 50% of population) 5.7 (median, low population density) 3.6 (median, high population density)		Öhrn et al. 2014
<i>Ips confusus</i>			1.3–1.5 m·s ⁻¹	Gara 1963
<i>Ips calligraphus</i>	Flight mill	1.7 (mean) 0.05–6.4 (total range)	0.54–2.9 (total range)	Kinn 1986
<i>Ips grandicollis</i>	Mark–recapture	0.06 (mean)		Costa et al. 2013
<i>Hylurgus ligniperda</i>	Mark–recapture	>0.96, highest capture at 0.040		Meurisse and Pawson 2017
<i>Pityophthorus juglandis</i>	Flight mill	0.37 (mean)	0.61 (mean)	Kees et al. 2017

Note: Data have been converted from their original units to units of km and km·h⁻¹ for comparative purposes.

(Gitau et al. 2013). Once the host is successfully colonized, bark beetles produce anti-aggregation pheromones to deter conspecifics from subsequent colonization (Raffa et al. 2015). In solitary species that do not mass attack tree hosts such as *Dendroctonus micans* (Kugelann) (Gilbert et al. 2001), beetles mate underneath the bark of the natal host, and new tree hosts are subsequently colonized by mated individuals after a dispersal flight (Raffa et al. 2015). Some species of bark beetles mass attack host trees. Mass attack of host trees by bark beetles in the epidemic population phase can impact landscapes and kill stands of healthy trees. Much of the research on bark beetle flight focuses on these tree-killing species in an effort to understand the spread of attack under outbreak conditions or range expansion, but knowledge gaps exist on the impact of population phase on flight behaviour.

As bark beetles are both ecologically and economically important, an understanding of this crucial life history trait is important to predict spread and manage tree-killing bark beetle species (Goodsman et al. 2016). In this review, we synthesize published literature on bark beetle flight capacity and dispersal, using information from the genetic level to the landscape level. We begin with a review of empirical data on flight capacity and the various tools used to measure bark beetle flight and model population spread. We then examine beetle morphological and physiological traits and both abiotic and biotic environmental factors that impact flight. Although the response to semiochemical cues during flight in bark beetles is well studied and is important to understanding host colonization and population spread, most of the research reviewed here focuses on flight capacity and dispersal rather than oriented flight. We emphasize flight studies on tree-killing bark beetles, primarily in the genera *Dendroctonus* and *Ips*, to compare and contrast the flight characteristics of species in these groups. With a comprehensive review of the factors that influence dispersal by flight and how dispersal is measured, we identify areas of future research required to inform predictive spread models for management of bark beetle populations.

1.1. Flight capacity

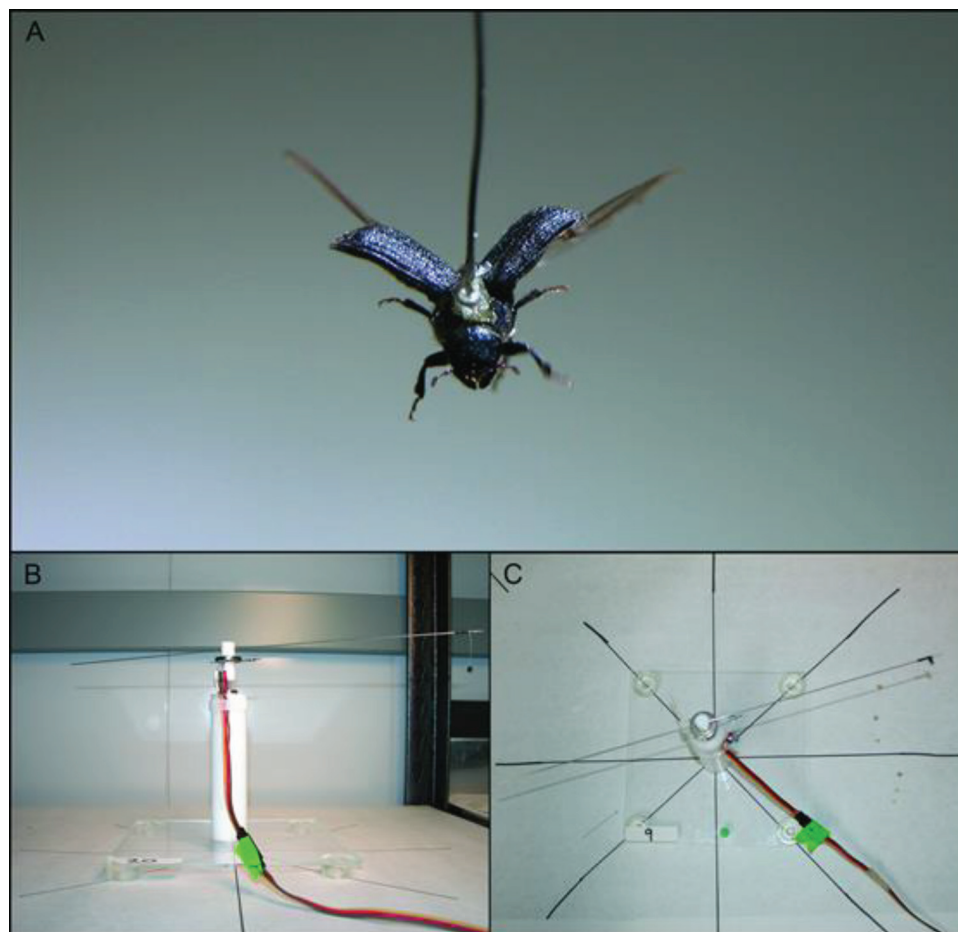
The terms “flight capacity” and “dispersal” are used interchangeably in the literature, but in this review, we distinguish between the two terms. Flight capacity is influenced by the energetic state of individual beetles, which relates to the size and energy stores of each beetle. Dispersal within a forest stand over short distances includes flight capacity and the impacts of exogenous factors such as environmental conditions, stand characteristics, and semiochemical cues on movement behaviour. Long-distance dispersal is characterized by above-canopy flight in which beetles do not actively fly but are carried by the wind.

Flight capacity varies greatly within and among bark beetle species (Table 1). Even within a population, bark beetle flight phenotypes can range from non-flyers to beetles that conduct exceptionally long flights (Evenden et al. 2014), which can extend over 50 km on flight mills (Jactel and Gaillard 1991). For example, flight capacity of *Dendroctonus ponderosae* Hopkins on flight mills ranges, on average, from 2.12 to 5.95 km; however, individuals have been recorded to fly greater than 24 km (Evenden et al. 2014). Although much of this variation can be explained by morphological or physiological factors, some may be genetic, but specific genes that dictate flight capacity in bark beetles have yet to be discovered. Flight mill studies of *D. ponderosae* illustrate that beetles with similar body condition, size, and mass still exhibit variable flight capacity (Shegelski et al. 2019). Multiple approaches to measuring flight capacity and dispersal are required to get an accurate view of dispersal by flight in bark beetles.

1.2. Measuring flight capacity and dispersal

Both direct and indirect methods have been developed to measure flight capacity and dispersal of bark beetles. Each method has its benefits and drawbacks, and no single method can mimic natural flight behaviours perfectly. Several methods combined, however, can complement each other to accurately measure flight and predict movement in bark beetles.

Fig. 1. (A) *Dendroctonus ponderosae* adult with tether affixed to pronotum. Flight mill with tether attached in (B) side and (C) aerial view. Previously published in Evenden et al. 2014, *Environmental Entomology*, 43(1): 187–196, doi:10.1603/EN13244. Reproduced with permission. [Colour online.]



Actual flight capacity of bark beetles has most commonly been measured under laboratory conditions with computer-linked flight mills. Flight mills consist of a rotational arm suspended above a central pivot point (Robertson and Roitberg 1998). The beetle is suspended from one end of the arm using a tether that is attached in some manner to the insect's pronotum (Evenden et al. 2014) (Fig. 1). Every rotation of the arm is recorded via sensors connected to a computer (Robertson and Roitberg 1998). Flight mills can be used to measure flight capacity of beetles with different flight phenotypes, which is more difficult to obtain with other flight measurement methodology. Although this technique is useful for measurement of flight propensity, capacity, distance, and velocity, it cannot be used to measure oriented flight. Exposure of beetles to volatile chemical cues during flight mill bioassays provides a way to measure the impact of semiochemicals on flight propensity (Bennett and Borden 1971) and turning during flight (Hughes and Pitman 1970), but the restriction of the tether prevents oriented flight.

Bark beetles are normally attached to the flight mill arm with a stiff tether, but soft flexible tethers are also used (Blackmer et al. 2004). Stiff tethers suspend the beetle so that they do not carry their full body mass. Insects on stiff tethers can be forced to initiate flight as a result of suspension on the mill and loss of tarsal contact with the substrate (Wilson 1961). The stiff tether can also negatively impact insect flight on flight mills, as the insect must overcome inertia associated with attachment to the mill arm (Taylor et al. 2010). As a result, some studies suggest that dispersal measurements of flight on flight mills may be overestimated

(Robertson and Roitberg 1998), while others suggest that dispersal capacity is underestimated (Taylor et al. 2010). For this reason, among others, flight data generated on flight mills can only be used in a relative and not an absolute manner. The relative differences between test subjects (male vs. female, young vs. old, fed vs. starved) should be consistent between tethered and free flight as long as there is no interaction between the effect of the tether and the treatment under study (Taylor et al. 2010). Free flight of emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), occurs at velocities $\sim 3\times$ as fast as those on flight mills and can be used to calibrate flight mill studies and obtain absolute dispersal capacities (Taylor et al. 2010). Future bark beetle flight studies should attempt to calibrate flight on mills with measurements of free flight.

Common methods to study dispersal by flight in natural habitats include mark–recapture experiments and capture of dispersing bark beetles in semiochemical-baited traps (Linton et al. 1987; Safranyik et al. 1989, 1992; Zumr 1992; Barclay et al. 1998; Franklin and Grégoire 1999). Mark–recapture involves the collection or rearing of the target insect followed by the release of marked individuals at a specific location. Bark beetles have been marked externally with paint or coloured powder or by elytra engraving (Jactel 1991; Duelli et al. 1997; Barclay et al. 1998; Reid and Reid 2008; Doležal et al. 2016) prior to release in forest stands. Application of powder to the outside of beetle-infested tree bolts allows for passive marking of beetles as they emerge from the bolt. Passive marking reduces handling time and increases the number of beetles that can be marked (Reid and Reid 2008; Doležal et al.

2016). Marked beetles can be recaptured after release in passive traps (Safranyik et al. 1992), semiochemical-baited traps (Salom and McLean 1991; Doležal et al. 2016), or trap trees (Safranyik et al. 1992; Franklin and Grégoire 1999). Although important discoveries on flight under natural conditions can be drawn from mark-recapture experiments, they are logistically difficult to conduct. Large numbers of individuals need to be released, and often few are recaptured (Barclay et al. 1998; Franklin and Grégoire 1999). Further, trap placement can bias these studies, as individuals captured in the trap closest to the release site may still be capable of further dispersal (Yamamura et al. 2003). Therefore, mark-recapture experiments cannot measure flight capacity of non-fliers and long-distance fliers. Although difficult to conduct and interpret, mark-recapture field studies can provide information on minimum flight capacity and within-stand oriented flight. Mark-recapture data have been used to parameterize diffusion models of flight dispersal in the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Turchin and Thoeny 1993). Semiochemical-baited traps can measure the attraction of beetles to various cues and the occurrence of beetles in certain habitats. Beetle capture in semiochemical-baited traps, however, does not reflect beetle movement during the initial non-oriented phase of flight dispersal (Franklin and Grégoire 1999). These methods are reliable monitoring tools (Evenden and Silk 2016), but trap capture does not always reflect stand-level population density (Cronin et al. 2000).

A small proportion of some bark beetle populations disperse by flight at higher altitudes above the forest canopy. This type of movement can be measured with weather radar imagery (Jackson et al. 2008) and aircraft-mounted radar (Chapman et al. 2011). The latter uses a radar beam directed at the ground that is intersected by flying insects in the sampled airspace. As the insects cross the vertical beam, an echo is recorded that provides the height and speed of the flying insect (Chapman et al. 2011). Nets mounted to aircraft can also physically catch insects in flight at high altitudes to confirm species identity (Jackson et al. 2008). Above-canopy beetle dispersal is facilitated by meso-scale atmospheric currents rather than individual-beetle flight capacity. Under these conditions, terrain-induced currents influence dispersal distance and the potential for population establishment (de la Giroday et al. 2011). A long-range dispersal event of *Dendroctonus ponderosae* across the Rocky Mountains led to initial establishment of beetle populations on south-facing ridges, canyons, and valleys. Identification of landscape variables that influence air movement and subsequent beetle infestation (de la Giroday et al. 2011) should be a priority for forest research. Topographic position indices can be modelled across the landscape to prioritize management efforts in the invaded range.

Dispersal of tree-killing bark beetles across the landscape can be indirectly assessed after the fact through aerial surveys of dead and dying trees (Robertson et al. 2007) or with ground-truthing methods using a geographic information system (GIS) (Wichman and Ravn 2001). Aerial surveys and GIS are most effective when paired, and the data can be used to model population spread. Population genetic tools can also be used to understand the origin of new beetle outbreaks on the landscape and infer dispersal capacity to the new location (Trevoy et al. 2018). These methods do not produce data on actual flight capacity of individual beetles; however, they do produce an understanding of population movement and success of mass attack.

1.3. Modelling dispersal

Measurement of beetle movement in real time is difficult, so much effort has focused on indirect methods such as modelling potential dispersal that can be verified with subsequent field observations on population spread across the landscape (Robertson et al. 2007; Lundquist and Reich 2014; Liang et al. 2017; Powell et al. 2018). The energetic state or condition of individual beetles (Chubaty et al. 2009) and the flight settling rate, the rate at which

beetles cease flight activity (Kautz et al. 2014, 2016; Goodsmann et al. 2016), inform and parameterize bark beetle movement models. More recently, genetic tools have been adopted to map range expansion of bark beetle populations (Mock et al. 2007; Cullingham et al. 2012; Samarasekera et al. 2012), including the use of integrated landscape genetics techniques (James et al. 2011).

A popular framework for modelling population spread is the use of dispersal kernels. Dispersal kernels are functions that give the probability of individuals within a population moving from one point to another. The form of a given dispersal kernel is traditionally dictated by a probability density function. Dispersal kernels model well-known dispersal processes such as diffusion, biased random walks, and Lévy flights (Petrovskii et al. 2008). Models for dispersal kernels include many complicated factors such as density dependence (French and Travis 2001; Lutscher 2008) and spatial heterogeneity (Dewhurst and Lutscher 2009; Vinatier et al. 2011). The ability to include biological complexities in models using a dispersal kernel is an advantage when modelling population spread.

Dispersal kernels fit along a spectrum between thin-tailed and fat-tailed kernels. Thin-tailed dispersal kernels account for short-distance dispersal events where offspring settle near their parents' range, whereas fat-tailed dispersal kernels are used for modelling long-distance dispersal events. Short-distance dispersal is the result of an individual's inherent movement, whereas long-distance dispersal is mediated by some form of passive transport (Shigesada and Kawasaki 2002). In general, short-distance dispersal events are more common than long-distance dispersal events. Although long-distance dispersal events are rare, they can have a profound effect on dispersal patterns of the population under study. Rare long-distance dispersal events can cause patchy invasions and acceleration of spread of an invasive population (Clark et al. 2001). The use of a mixed dispersal kernel in modelling efforts can be beneficial to include both short- and long-distance dispersal events. Mixed dispersal kernels assume that a proportion of the population spread occurs according to a thin-tailed dispersal kernel and the remaining spread follows a fat-tailed dispersal kernel (Clark 1998). The skewness and kurtosis of dispersal kernels are important factors in the calculation of spread rates of a population (Lockwood et al. 2002). The asymmetries in dispersal are informed by skewness, which accounts for events such as advection due to wind but does not provide information about the tail shape of the dispersal kernel. Kurtosis provides a measure of the "tailedness" of the distribution, which can greatly influence population spread rates (Lockwood et al. 2002). The kurtosis is directly related to the fatness of the tail, that is, a higher measure of kurtosis results in a dispersal kernel with a fatter tail. Distributions with fatter tails than the univariate normal distribution are called leptokurtic, whereas distributions with thinner tails than the univariate normal distribution are called platykurtic. Thus, leptokurtic kernels model individuals with a higher probability of long-distance dispersal that produce faster invasion speeds than platykurtic distributions (Kot et al. 1996). Because of the prevalence of long-distance dispersal of bark beetle populations, the applicability of fat-tailed dispersal kernels to bark beetle spread models needs to advance beyond simulations.

2. Morphology

2.1. Body mass

The effect of bark beetle body mass on flight capacity is important for many of the species studied to date (Atkins 1966; Bennett and Borden 1971; Evenden et al. 2014). Beetle mass is directly related to the amount of energy available in some beetles (Thompson and Bennett 1971; Chen et al. 2011; Evenden et al. 2014) and is highly variable both among and within bark beetle species. Adult body mass can be affected by beetle density in the natal host (Anderbrant and Schlyter 1989), larval competition (Atkins 1975),

temperature during development (Sahota and Thomson 1979), development time (Mori et al. 2011; Graf et al. 2012), tree diameter (Graf et al. 2012), phloem quality (Anderbrant and Schlyter 1989), and nutrition (Ayres et al. 2000; Bleiker and Six 2007). Most studies agree that body mass is an important component of beetle energy state (Bennett and Borden 1971; Anderbrant and Schlyter 1989; Latty and Reid 2010; Esch et al. 2016) and is correlated with lipid content (Thompson and Bennett 1971; Graf et al. 2012) and flight capacity (Kinn et al. 1994; Chen et al. 2011; Evenden et al. 2014).

There appears to be three main ways in which beetle mass influences flight performance. Heavier beetles (i) display an increased propensity to fly (Atkins 1966; Jactel 1993; Evenden et al. 2014), (ii) can have reduced response to olfactory cues before flight metabolism, resulting in prolonged dispersal bouts (Atkins 1966; Bennett and Borden 1971), and (iii) have more energy to sustain long-term flight (Thompson and Bennett 1971; Williams and Robertson 2008). The propensity to fly can affect dispersal for obvious reasons, as beetles that do not initiate flight will not disperse. Once flight is initiated, body mass influences flight distance in bark beetle species from various genera, including *Ips* (Schlyter and Löfqvist 1986), *Dendroctonus* (Bennett and Borden 1971), and *Scolytus* (Choudhury and Kennedy 1980). In general, large beetles fly farther than small beetles (Atkins 1975; Slansky and Haack 1986; Evenden et al. 2014). Flight response of *Dendroctonus pseudotsugae* Hopkins is dependent on lipid content, which is correlated with body mass (Atkins 1966, 1975). As lipid content cannot be measured prior to experimental studies but is destructively sampled after the fact, mass is sometimes used as a proxy for lipid content. Not all studies of bark beetle flight illustrate an effect of body mass on flight capacity. The body mass of *Ips typographus* (Linnaeus) has no influence on flight capacity as measured in a mark-recapture study (Botterweg 1982). Although mark-recapture studies may present beetles with natural flight conditions, other factors besides flight distance may influence the lipid content and body mass of the measured beetles. Even under laboratory conditions, body mass and lipid content are not always related to flight capacity. During a 5 h flight mill bioassay in which fat oxidation in flight was quantified, the flight capacity of *D. pseudotsugae* was not dependent on beetle body mass or lipid content (Thompson and Bennett 1971). The relationship between lipid content and flight capacity in *D. pseudotsugae* became apparent when longer assays were used (Williams and Robertson 2008). Longer flight bioassays are often needed (Atkins 1960) to reliably record the relationship between body mass and flight in some bark beetles (Chen et al. 2011; Evenden et al. 2014).

Some confusion exists in the literature surrounding the significance of body mass on beetle flight because of the common use of the term “body size”, which can refer to body mass or other morphological measurements of size. Jactel (1993) uses pronotum width as a proxy for body size; Botterweg (1982) and Forsse and Solbreck (1985) use elytra mass and length, respectively; and studies by Evenden et al. (2014) and Anderbrant and Schlyter (1989) use beetle mass. It is important to distinguish between these terms as physical body dimensions often do not predict flight capacity of individual bark beetles (Botterweg 1982; Forsse and Solbreck 1985; Jactel 1993; Shegelski et al. 2019).

2.2. Sexual size dimorphism

Some species of tree-killing bark beetles exhibit sexual size dimorphism (Hulcr et al. 2015), which contributes to variation in flight capacity by sex in some bark beetles (Slansky and Haack 1986; Kinn et al. 1994) but not others (Evenden et al. 2014). Host tree colonization is initiated by the pioneer sex, and sexual size dimorphism leading to variable flight can affect colonization dynamics (Schlyter and Löfqvist 1986; Hulcr et al. 2015). In cases of flight variation due to sexual size dimorphism, the larger sex has greater flight capacity than the smaller sex (Kinn et al. 1994) due to greater energy reserves (Evenden et al. 2014). Sexual size dimor-

phism occurs in some economically important bark beetles such as *Ips pini* (Say), *Ips lecontei* Swaine, *Dendroctonus frontalis*, *Dendroctonus brevicomis* LeConte (Foelker and Hofstetter 2014), and *Dendroctonus ponderosae* (Hay 1956). In these examples, sexual size dimorphism favours the pioneering sex, resulting in larger female *Dendroctonus* and larger male *Ips* (Schlyter and Löfqvist 1986; Hulcr et al. 2015).

Body mass does not always influence flight capacity in bark beetle species in which males pioneer the host colonization process (Schlyter and Löfqvist 1986). Of the *Ips* species for which flight capacity has been tested, only *Ips calligraphus* (Germar) and *Ips sexdentatus* Boerner display male-biased sexual size dimorphism, and a positive effect of body mass on flight only occurs in *I. calligraphus* (Slansky and Haack 1986). Male *I. calligraphus* have greater flight capacity than females due to large body size and greater lipid stores, which may promote host location and colonization at a distance from the natal host (Slansky and Haack 1986). Other work shows no effect of beetle sex on flight in *I. calligraphus* (Kinn 1986); however, the lack of significance in this study may be due to low sample size. In general, there is little evidence for an effect of body mass on flight capacity in bark beetle species with male pioneers (Botterweg 1982; Jactel 1993). Sex and a variety of body size measurements do not influence flight capacity in either *I. typographus* (Botterweg 1982; Forsse and Solbreck 1985) or *I. sexdentatus* (Jactel 1993). In *Ips*, mass attacks are initiated by males but completed by both males and females. Jactel (1993) hypothesized that similar flight performance by both sexes would promote large aggregations during host colonization. Both sexes are involved in pheromonal aggregation and mass attacks, and similar flight performance of males and females may lead to more individuals colonizing hosts within a similar dispersal range, potentially resulting in increased mass attack densities.

In contrast, beetle body mass seems to play an important role in flight capacity in sexually dimorphic species in which females are the pioneering sex. In these species, beetle body mass is correlated with stored energy content (Kinn et al. 1994; Evenden et al. 2014). Larger beetles have greater flight capacity in species such as *Dendroctonus frontalis* (Kinn et al. 1994), *D. pseudotsugae* (Williams and Robertson 2008), and *D. ponderosae* (Evenden et al. 2014). These species have female-biased sexual size dimorphism. Although female beetles are bigger in many *Dendroctonus* species, it is important to note that the effect of body mass on flight is often not sex-specific and flight capacity does not significantly differ based on sex (Atkins 1961; Kinn 1986; Evenden et al. 2014).

Sexual size dimorphism occurs in several species such as *I. pini* and *D. brevicomis* (Foelker and Hofstetter 2014) for which sex-biased flight capacity has not yet been investigated (Hulcr et al. 2015). Flight differences between sexes may be difficult to identify in some species of bark beetle. In *Dendroctonus armandi* Tsai & Li, there is no sexual size dimorphism and no significant effect of sex on daily flight, but females fly ~600 m further than males in a 96 h bioassay (Chen et al. 2011). In some species, there appears to be a direct effect of sex on flight in the absence of sexual size dimorphism (Chen et al. 2010, 2011). The mechanisms driving these differences remain to be identified, but there is evidence for sex-specific use of different energy substrates in some bark beetles (Pitt et al. 2014; Wijerathna 2016). It is also possible that sex-based differences in sustained flight are masked during lab flight bioassays. Flight bioassays in the laboratory are of variable duration in different studies. Beetles have been flown for 5 h (Thompson and Bennett 1971), 23 h (Evenden et al. 2014), 96 h (Chen et al. 2011), or until exhaustion (Slansky and Haack 1986). Assays that more closely mimic natural dispersal and incorporate periodic flights spanning multiple days may be more relevant to estimation of below-canopy dispersal events conducted by most individuals in bark beetle populations (Forsse and Solbreck 1985; Jactel and Gaillard 1991; Evenden et al. 2014) that might reveal sex-based differences.

2.3. Wing size and shape

Wing beat frequency and amplitude are closely integrated with lift of flying insects (Atkins 1960; Casey 1989); these traits must both be controlled to produce optimal lift for flight (Altshuler et al. 2005). While wing-beat frequency is mostly influenced by environmental conditions such as temperature (Oertli 1989), flight muscle and wing morphology also impact wing-beat frequency and, subsequently, flight capacity. Wing beat frequency increases with wing loading (body mass/wing area), inertia, and resistance. Bark beetle wing size and shape influence these measures and affect wing-beat frequency (Atkins 1960) and subsequent flight capability (Shegelski et al. 2019). Wing area is one of the most important morphological factors that influence flight capacity in *D. ponderosae* (Shegelski et al. 2019).

Bark beetles also use wing movements to decelerate and land in appropriate habitats (Bennett and Borden 1971). Flight arrestment of *D. pseudotsugae*, as observed on flight mills, includes wing folding with quick closure of the elytra. Beetles also display a variety of gliding behaviours, including planing, flexing, and vibrating outstretched wings (Bennett and Borden 1971). These flight behaviours may increase the potential for wind-assisted long-distance dispersal; wing size, shape, and position are important for the dispersal of winged seeds in plants (Augspurger 1986), but this has yet to be investigated in passive dispersal of bark beetles.

2.4. Flight muscle

Insect flight muscle must comprise 12%–16% of body mass to support flight. In general, flight muscle size varies with flight capacity, as large flight muscles are correlated with increased lift and acceleration in insect flight (Marden 2000). Maintenance of bark beetle flight muscles is plastic so that resources can be redirected between periods of flight. Flight muscles degrade after a successful attack on a host, which allows for a reallocation of resources to reproduction (Atkins and Farris 1962; Bhakthan et al. 1970). In *Ips* species, muscle degeneration and resource reallocation are pronounced and prolonged in mated individuals, especially in females before brood production (Borden and Slater 1969). Degeneration is the result of a reduction in the size of the dorsal longitudinal and dorsoventral indirect flight muscles (Atkins and Farris 1962; Langor 1987). Concomitant with muscle degeneration is an increase in gonad size that can displace flight muscles in reproducing females (Atkins and Farris 1962). In some species, flight muscle degradation occurs within a week of host colonization (McCambridge and Mata 1969) but can take place as quickly as 1–2 days after attack (Chapman 1956; Atkins 1959; Atkins and Farris 1962; Borden and Slater 1969). Flight muscle degeneration in bark beetles is due to activation of lysosomal activity (Bhakthan et al. 1970) triggered by an elevated titre of juvenile hormone (Borden and Slater 1969; Sahota 1975; Unnithan and Nair 1977). Degradation of flight muscles is a common energy-saving mechanism that occurs in many species of bark beetles, including *D. ponderosae* (McCambridge and Mata 1969), *D. pseudotsugae* (Atkins 1959), *Dendroctonus rufipennis* Kirby (Sahota and Farris 1980), *Dendroctonus simplex* LeConte (Langor 1987), *Hypothenemus hampei* (Ferrari) (López-Guillén et al. 2011), *Ips confusus* (LeConte) (Borden and Slater 1969), *Ips paraconfusus* Lanier (Unnithan and Nair 1977), *I. typographus* (Forsse and Solbreck 1985), and *I. pini* (Robertson 1998).

Bark beetles can regenerate flight muscles to perform subsequent dispersal events (Bhakthan et al. 1971; Langor 1987). Some species such as *D. ponderosae* show muscle regeneration in the majority of individuals (McCambridge and Mata 1969) after reproduction. Only ~15% of *D. simplex*, however, fully recover flight muscle after the short reproductive season in Newfoundland, Canada (Langor 1987). Although the potential for a second dispersal flight is acknowledged for many bark beetles (Atkins 1961; Botterweg 1982; Langor 1987), the importance of this flight on dispersal and range expansion has received little attention. Dis-

persal flights after reproduction by *D. pseudotsugae* are longer than initial flights (Atkins 1961), which may be attributed to better phloem quality in the reproductive host over the natal host (Atkins 1961). Better nutrition through access to fresh, high-quality phloem increases dispersal capacity in bark beetles (Slansky and Haack 1986; Anderbrant and Schlyter 1989; Chen et al. 2011). In contrast, flight after re-emergence in *Ips typographus* is generally similar to (Botterweg 1982) or shorter than (Zolubas and Byers 1995) the distance of initial dispersal flights of overwintered beetles that emerge from the soil. Diapausing *D. pseudotsugae* and *I. typographus* adults have underdeveloped flight muscles compared with non-diapausing adults (Ryan 1959, Doležal and Sehnal 2007).

2.5. Evaluation of morphological factors on flight

Bark beetle flight studies assess a variety of morphological factors that could impact flight capacity. Of the morphological factors examined to date, body mass explains the most variation in flight capacity. Although high body mass increases wing loading, larger insects have more energy to fuel flight. The correlation between mass and flight capacity is stronger in *Dendroctonus* than in *Ips*. Body mass and not beetle sex drives flight capacity in most sexually dimorphic bark beetles. Flight muscle size also correlates with flight capacity in bark beetles. Wing shape and size contributes to flight capacity in some bark beetles (Shegelski et al. 2019), but research into specific genes coding for wing structure is lacking. Flight muscle size seems to be equally important in the prediction of flight capacity in both *Dendroctonus* and *Ips*, suggesting that the energetic capacity of large *Dendroctonus* beetles is a key driver of flight capacity. Future research should focus on relating muscle mass and volume to determine which measurement is more accurate for predicting flight capacity.

3. Physiology

3.1. Genetics

There is a lack of research on the genetics of flight in bark beetles; however, hints at important flight genes can be gained from bark beetle population structure and gene flow using population and landscape genetics tools. The genetics associated with range expansion in *D. ponderosae* reveal several informative patterns and isolation by distance (reviewed by Cullingham et al. 2019). More research is needed on the landscape genetics of other bark beetle species undergoing range expansion to determine if the patterns discovered for *D. ponderosae* are common in other species.

Patterns of landscape-level isolation by distance occur in *D. ponderosae* populations in the United States (US), except in regions such as the Mojave Desert (Mock et al. 2007) where barriers to dispersal occur. Northern US populations of *D. ponderosae* experience mutation retention and low genetic diversity, which indicate recent range expansion (Mock et al. 2007). Heritability and variation of important life history traits such as developmental time and body size (Bentz et al. 2011) might also influence dispersal by flight, even though they do not follow isolation by distance patterns on the landscape (Mock et al. 2007; Bracewell et al. 2013).

Genetic population structure of the northernmost *D. ponderosae* populations in western Canada support two distinct *D. ponderosae* populations (northern and southern) and a genetically intermediate population (Samarasekera et al. 2012; Janes et al. 2014; Batista et al. 2016). The intermediate population is closely related to lab-produced hybrids of the northern and southern populations (Trevoy et al. 2018). This indicates genetic admixture, which has important implications for management as hybridization may generate novel, potentially adaptive, genetic elements (Rieseberg and Burke 2001) that may be related to flight and dispersal.

Genetic adaptation relating to flight in bark beetles has not yet been specifically addressed in the literature, but work by Janes et al. (2014) and Batista et al. (2016) have identified several genes

that appear to be under selection within the range of *D. ponderosae* in western Canada. These genes may be related to flight through the modification of related cellular, muscular, and metabolic functions; however, the actual effects of these genes and any potential effects on *D. ponderosae* flight have not been specifically tested.

Although flight genes have not been identified in bark beetles, there are several examples of genes linked to flight and dispersal phenotypes in other insect groups. For example, glucose-6-phosphatase (G6Pase) and phosphoglucose isomerase (PGI) are both partially responsible for the regulation of metabolic rate (Montooth et al. 2003; Niitepold et al. 2009; Wheat et al. 2010), and PGI has also been linked to improved flight in adverse conditions (Niitepold et al. 2009; Wheat et al. 2010). Succinate dehydrogenase (Sdh), which relates to tracheation in muscles (Marden et al. 2012), and *four-jointed* (*ff*) and *dachsous* (*ds*) genes, which affect wing growth patterns in *Drosophila* (Rogulja et al. 2008), may also contribute to dispersal capabilities in bark beetles. Expression of the locust foraging gene, *for*, which encodes a cGMP-dependent protein kinase (PKG) enzyme activity, appears to affect dispersal phenotypes in the desert locust *Schistocerca gregaria* Forsskål (Lucas et al. 2010). On-going studies on gene expression of strong and weak flight phenotypes of *D. ponderosae* (V.A. Shegelski, M.L. Evenden, and F.A.H. Sperling, 2018, unpublished) have identified several metabolic and behavioural genes that are differentially expressed in beetles based on flight experience. Similar methods have been used by Jones et al. (2015) to identify genes related to migratory flight phenotypes in the cotton bollworm, *Helicoverpa armigera* Hübner.

The genetics of the host colonization process following dispersal by flight has been examined in some bark beetle species. Transcriptomic studies of *D. ponderosae* reveal important physiological processes involved with successful establishment, including detoxification of host defenses and reproduction during host colonization (Huber and Robert 2016) and biosynthesis of cryoprotectants such as glycerol in overwintering larvae (Robert et al. 2016; Fraser et al. 2017). Although these genes are not likely to directly impact flight, flight and host colonization behaviours are closely linked and these systems are important for successful host establishment after dispersal.

Several studies have used population genetics to understand population structure and gene flow in *D. ponderosae* (Cullingham et al. 2019). Other studies have identified potentially adaptive loci that contribute to our understanding of the spread of *D. ponderosae* across the landscape (Janes et al. 2014; Batista et al. 2016); however, the specific genes relating to flight in bark beetles and any associated physiological mechanisms remain unknown. Thousands of genes may affect bark beetle flight, and this is a vast area of research that should be explored to further our understanding of bark beetle flight capacity and dispersal.

3.2. Lipids

Lipids are the major source of energy used during bark beetle flight, and triglycerides make up the majority of this energy source (Kinn et al. 1994). Energy use during flight has been studied in laboratory settings, where beetle lipid content is assessed after flight on flight mills and compared with that of control beetles that have not flown (Atkins 1969; Thompson and Bennett 1971; Williams and Robertson 2008; Chen et al. 2011; Evenden et al. 2014). Pre-flight lipid levels cannot be directly assessed due to the destructive nature of lipid extraction. Models, however, can be used to relate beetle lipid content after flight, time spent in flight, and time in non-flight activities to predict lipid content before flight (Williams and Robertson 2008). Lipids fuel long-distance flight of bark beetles (Chen et al. 2011), as the lipid content of beetles that exhibit sustained flight is lower compared with the non-flown control beetles (Atkins 1969; Thompson and Bennett 1971; Williams and Robertson 2008; Evenden et al. 2014).

Flight capacity of bark beetles is related to body lipid content, as individuals with more lipids fly further distances (Kinn et al. 1994; Williams and Robertson 2008; Chen et al. 2011; Evenden et al. 2014) and for longer durations (Hodges and Barras 1974; Kinn et al. 1994; Williams and Robertson 2008; Chen et al. 2011) compared with beetles with low lipid content. In *D. armandi*, there is a positive relationship between body lipid content and total flight distance and duration (Chen et al. 2011). *Dendroctonus pseudotsugae* with high lipid reserves fly further and longer than beetles with low reserves (Williams and Robertson 2008); those with less than 10% lipid content will not initiate flight (Atkins 1966). *Dendroctonus ponderosae* uses stored lipids obtained from feeding in the natal habitat during the obligatory flight dispersal period (Thompson and Bennett 1971; Bentz 2006; Evenden et al. 2014). The lipid content of *D. frontalis* after flight is negatively correlated with beetle flight duration and distance (Hodges and Barras 1974; Kinn et al. 1994). Lipids are metabolized during *D. frontalis* flight by the degradation of triglycerides into short-chain fatty acids, a process that occurs between adult emergence from the natal host and subsequent host colonization (Hodges and Barras 1974). There is some evidence for selective oxidation of certain fatty acids during flight of *D. pseudotsugae*. Monounsaturated 16- and 18-carbon fatty acids are oxidized at the highest rate during flight of male beetles, which may simply reflect the abundance of these compounds in the overall fatty acid profile of these insects (Thompson and Bennett 1971).

Most bark beetles do not exhaust stored lipid reserves during dispersal by flight (Thompson and Bennett 1971; Gast et al. 1993; Williams and Robertson 2008). Some fat is retained, likely because energy is required for host colonization and reproduction. Fat content contributes to beetle energetic state, which subsequently dictates host colonization behaviour in bark beetles (Chubaty et al. 2009, 2014). Individual *D. ponderosae* with low lipid reserves are less selective and accept poorer quality host trees sooner than do individuals with high lipid reserves that are capable of continued dispersal (Chubaty et al. 2009, 2014; Latty and Reid 2010). There is also a positive correlation between lipid content and host colonization success in *Ips pini* (Wallin and Raffa 2000). Lipid use during flight can impact the host colonization process directly; beetles that fly may be more vulnerable to tree defenses, as beetles need lipids to overcome exposure to monoterpenes (Reid et al. 2017).

Lipids are required for host colonization behaviours in *Ips pini* (Gast et al. 1993; Wallin and Raffa 2000), but there is mixed evidence to support a correlation between lipid content and flight capacity in *Ips* studied to date. The relative lipid content of *I. sexdentatus* and *I. typographus* is not correlated with flight duration (Jactel 1993; Zolubas and Byers 1995; Schilling et al. 2012). *Ips sexdentatus* beetles that fly, however, have significantly higher lipid content than non-flyers. This could indicate that a lipid content threshold is needed to initiate flight in this species. In addition, there is a positive correlation between lipid content and long-distance flight in *I. sexdentatus* (Jactel 1993). In *I. typographus*, lipids are consumed during long-distance flight; however, lipid metabolism is disproportionately low (Schilling et al. 2012), suggesting that other energy sources may be used in addition to lipids to power flight in *Ips* species. Re-emergence from the reproductive host for a second flight period is related to lipid content in *I. typographus* (Zolubas and Byers 1995). Males that re-emerge for a second dispersal flight have more lipid, on average, than initial attackers (Botterweg 1982). This may indicate that only a subpopulation of the original colonizers have adequate energy to conduct a second flight (Botterweg 1982). It is important to understand the proportion of insects that conduct a second dispersal flight, as it will impact population spread of this outbreaking species.

3.3. Carbohydrates

Lipid metabolism to fuel flight has been relatively well studied in bark beetles, but less information is available on the use of other energy sources in the energy budget (Němec et al. 1993). Wood-feeding insects obtain carbohydrates from digestion of the primary and secondary cell wall polysaccharides of plant tissue (Mason et al. 2016). Bark beetles colonize trees with phloem rich in glucose and fructose (Ilse and Hellgren 2007), and beetle glucose content increases with prolonged phloem feeding (Chen et al. 2011). Carbohydrates are energy rich and can be important in fueling demanding activities such as flight.

Insects use glucose (Chen et al. 2011; Wijerathna 2016) and trehalose (Wijerathna 2016), the main blood sugars in insects, for flight initiation (van der Horst et al. 1980; Kaufmann and Brown 2008). In early work on *D. pseudotsugae*, measurement of the respiratory quotient of male beetles during flight indicated that carbohydrate, in addition to lipid, is used during the initial stages of flight in this species (Thompson and Bennett 1971). Later work used the hot anthrone method (Van Handel 1985) to directly measure carbohydrate content of flown and control *D. armandi* (Chen et al. 2011). Although carbohydrate sources of energy are thought to be most important in initial flight behaviours, glucose content of *D. armandi* declines with time in flight (Chen et al. 2011), indicating that glucose is an energy source used throughout the flight period. Trehalose content in *D. ponderosae* is lower after flight in both male and female beetles, but glucose powers flight only in females (Wijerathna 2016). More research is needed, however, to determine if these carbohydrate sources are utilized only during the initial flight stages or for sustained flight in *D. ponderosae*. The glycogen content of *D. ponderosae* (Wijerathna 2016) and *D. armandi* (Chen et al. 2011) is similar before and after flight, which is consistent with the idea that stored carbohydrates are not efficient energy sources for insect flight (Storey 1985). In contrast, some *Ips typographus* captured in pheromone-baited traps have low glycogen content compared with beetles caught in free flight using sweep nets, which is interpreted as carbohydrate use during long-distance flight (Němec et al. 1993). Relatively little research has been conducted on the use of carbohydrate sources in bark beetle flight, and it is a rich area for future research.

3.4. Proteins and amino acids

Proteins are not only used as the building blocks of flight muscles, but also can be metabolized during flight for energy in bark beetles. Female *I. sexdentatus* utilize proteins during swarming and mating periods and are able to create new proteins while feeding after flight (Lieutier 1984). *Dendroctonus ponderosae* larvae accumulate nervous system proteins in the spring, which may be a preparation for adult activities such as dispersal by flight and detection of semiochemicals (Bonnett et al. 2012). *Dendroctonus ponderosae* males, but not females, use proteins as energy during flight. Males flown on flight mills have lower protein content compared with unflown males (Wijerathna 2016). This finding is supported by proteomic analyses of *D. ponderosae* early in host colonization in which proteins used by male beetles differ from those used by females (Pitt et al. 2014).

The oxidation of the amino acid proline is important for flight in some insects (Candy et al. 1997) and especially beetles. Proline is generated in the fat body from fatty acids and is transported to muscles via the protein–alanine shuttle system (Candy et al. 1997). In *I. typographus*, proline content decreases rapidly with flight (Schilling et al. 2012). After only 10 min of flight, proline levels decline by 66% compared with levels in unflown beetles, which suggests that proline is an important energy source for flight initiation in this species (Schilling et al. 2012).

3.5. Beetle physiological state and semiochemicals

In this review, we primarily consider bark beetle flight capacity rather than oriented flight in response to semiochemicals. It is,

however, impossible to separate these two types of flight completely as beetle-powered flight primarily occurs during the host-searching and colonization process. Initial flight occurs with the wind until beetles sense and respond to volatile cues and commence upwind-oriented flight (Gray et al. 1972; Safranyik et al. 1992). The physiological state of individual bark beetles influences responsiveness to volatile semiochemical cues in some bark beetle species. Only a small proportion, roughly 25%–30%, of *I. typographus* respond to pheromone-baited traps immediately following emergence, but most of the population disperses by flight before landing on potential hosts (Němec et al. 1993). Electroantennogram bioassays conducted on *I. typographus* show the highest antennal responses to semiochemicals in beetles after flight experience for 0–5 h. Antennal responsiveness is lower in beetles that experience very long flights (24–48 h) (Duelli et al. 1997). There may be an underlying biological mechanism such as lipid body content that determines which individuals respond to semiochemicals immediately and which become long-distance dispersers (Duelli et al. 1997).

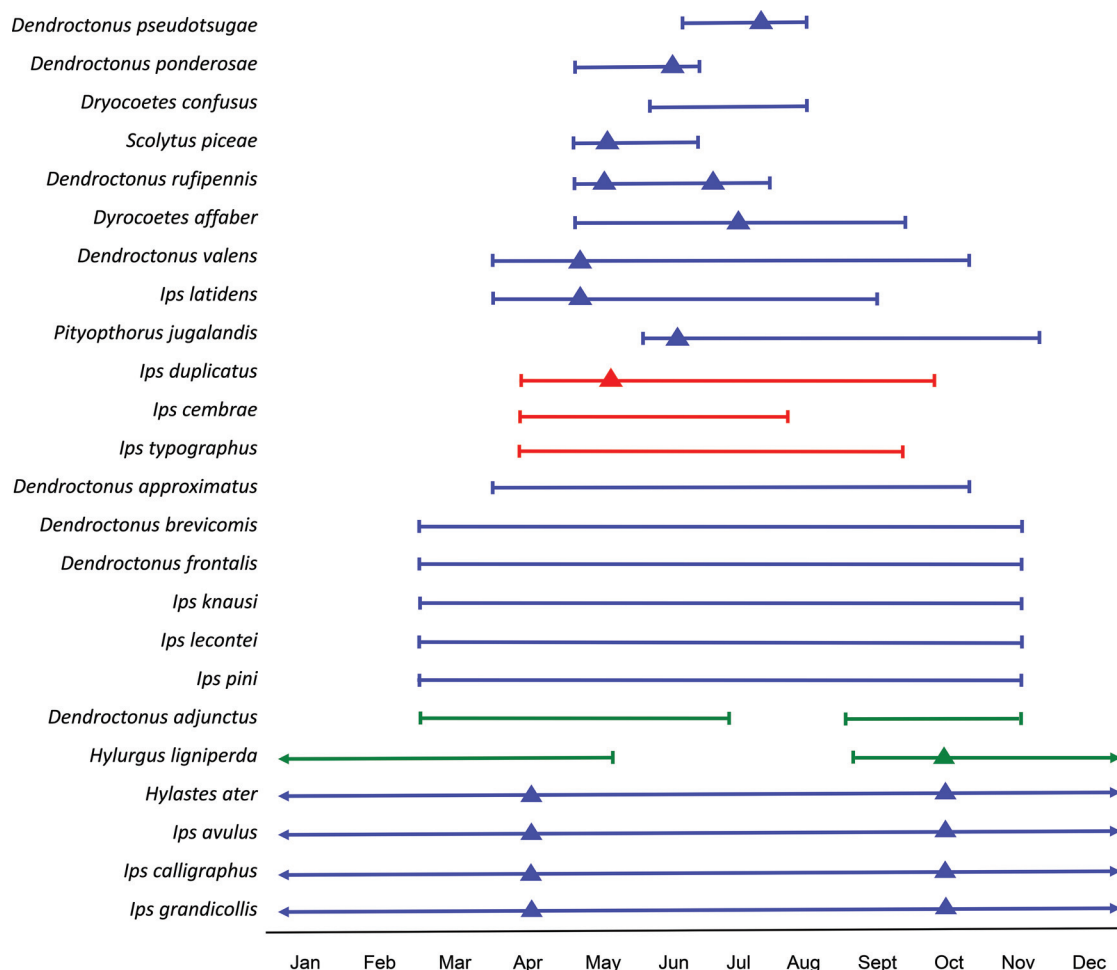
For certain species, beetle energetic state contributes to responsiveness to host kairomone or conspecific pheromone signals. *Dendroctonus pseudotsugae* females that respond to hosts have less lipids (15.83%) than those that are not responsive to host material (28.17%) (Atkins 1966). Metabolism of this stored energy through flight activity increases the likelihood that individuals will respond to host material. On average, *D. pseudotsugae* undergo 90 min of flight before eliciting a response to conspecific pheromone signals. Before this minimum flight threshold is reached, individuals seemingly ignore these chemical cues (Bennett and Borden 1971). Similarly, flight experience of *Hylurgus ligniperda* (Fabricius) increases orientation to pheromone traps (Meurisse and Pawson 2017). *Hylurgus ligniperda* with varying levels of previous flight experience are captured frequently in the first pheromone-baited traps that they encounter during flight, indicating rapid responsiveness to cues after flight (Meurisse and Pawson 2017). There may be evolutionary advantages to an internal feedback mechanism involving lipid oxidation that allows for a balance between dispersal distance and maintenance of physiological resources for host colonization (Bennett and Borden 1971).

Bark beetles with more than one generation per year experience different levels of nutrition at different times of the year, which could subsequently impact flight and response to semiochemicals between generations. More *I. paraconfusus* beetles in the summer generation respond to attractive chemical stimuli compared with beetles in the overwintered generation (Hagen and Atkins 1975). Similarly, beetles in the overwintering generation of *I. sexdentatus* fly, on average, 500 m farther than summer-generation beetles before orientation to semiochemical-baited traps (Jactel 1991). This pattern is attributed to higher lipid content in beetles in the overwintering generation compared with the summer-generation beetles. High lipid content of overwintered beetles contributes to greater dispersal capacity and longer flights before response to semiochemical cues (Hagen and Atkins 1975).

3.6. Evaluation of physiological factors on flight

Flight is an extremely beneficial but costly life history trait and requires a great amount of energy to initiate and sustain. Individual bark beetles even within the same population exhibit great variation in flight capabilities (Kautz et al. 2016). Part of this variation is due to the beetle physiological condition that is influenced by the quality of the natal host (Graf et al. 2012). Lipid metabolism appears to be important for understanding *Dendroctonus* flight variation. In studies conducted to date, flight capacity does not seem to be as strongly linked with lipid content in *Ips* species. Research on carbohydrate and protein metabolism in both *Dendroctonus* and *Ips* is sparse. Future work in this field should focus on understanding the timing of specific fuel usage during flight to determine what types of fuels are necessary for different types of

Fig. 2. Yearly flight activity of bark beetles as reported in the literature. Peaks in activity are indicated with triangles. Arrows indicate that flight does not stop from December–January. Blue indicates that flight activity was recorded in North America, green indicates that flight activity was recorded in South America, and red indicates that flight activity was recorded in Europe. Information was gathered from McMullen and Atkins (1962), Beckwith (1972), Hansen (1996), Mausel et al. (2007), Williams et al. (2008), Seybold et al. (2012), Schoeller and Allison (2013), Liu et al. (2014), Öhrn et al. (2014), and Bleiker and Van Hezewijk (2016). [Colour online.]



flight behaviour. Further gene discovery targeting flight metabolism and morphology in bark beetles, as has been shown for other insects, warrants investigation. Based on preliminary work on *D. ponderosae*, this approach seems promising and merits further pursuit.

4. Environmental factors

4.1. Abiotic

4.1.1. Temperature effects on phenology

Tree-killing bark beetles require synchronized flight activity to mass attack and colonize living trees (Raffa et al. 2015). Synchronization occurs through response to abiotic cues that dictate development, the timing of emergence from the host, and the commencement of dispersal flights (Safarynyk and Carroll 2006; Raffa et al. 2015). Flight and host colonization are generally limited by temperatures above flight thresholds that result in late spring and summer flight periods (Safarynyk and Carroll 2006; Weed et al. 2015). Some North American bark beetle species, including *Ips knausi* Swaine, *I. lecontei*, *I. calligraphus*, *Dendroctonus approximatus* Dietz, *D. frontalis*, and *D. brevicomis* (Williams et al. 2008), initiate flight in the early spring. The flight period duration is shorter at higher elevations and latitudes (Fettig et al. 2004; Williams et al. 2008) concomitant with cooler temperatures. Species such as *Ips grandicollis* (Eichhoff), *Ips avulsus* (Eichhoff),

I. calligraphus, and *Hylastes ater* Paykull that inhabit warmer regions are not limited by season and conduct several dispersal flights throughout the year (Mausel et al. 2007; Schoeller and Allison 2013). Two distinct peak flight periods can occur in spring and fall (Mausel et al. 2007; Schoeller and Allison 2013), which can indicate bivoltinism in the population. For example, the bivoltine species *Dendroctonus adjunctus* Blandford has spring and summer flights in Arizona that are comprised of individuals from different generations (Williams et al. 2008). Physiological and environmental factors may influence flight capacity of beetles in different generations. Flight capacity under controlled environmental conditions, however, is similar for individuals from the first and second generation of *D. armandi* (Chen et al. 2010).

In general, the flight activity period is longer in *Ips* species than in *Dendroctonus* species (Fig. 2). *Dendroctonus ponderosae* has a condensed flight period that lasts, on average, 26 days, which is one of the shortest recorded flight periods for a bark beetle (Williams et al. 2008; Bleiker and Van Hezewijk 2016). Aggressive bark beetle species are more likely to have short flight periods to coordinate the mass attack of host trees through the use of pheromone signals (Raffa et al. 2015). These species need to attack in unison to overcome host tree defenses, making a shorter, more synchronized flight period adaptive (Raffa et al. 2015).

Table 2. The flight temperature limits as reported from the literature of bark beetle species.

Species	Temperature (°C)			Citation
	Minimum	Optimal	Maximum	
<i>Dendroctonus pseudotsugae</i>	18.3 (initial flight)			McMullen and Atkins 1962
<i>Ips pini</i>	16.1 (initial flight) 11.7	17–38.9	>41	Gaylord et al. 2008
<i>Ips lecontei</i>	19 (initial flight) 15.2	19–38.9	>41	Gaylord et al. 2008
<i>Ips calligraphus</i>	21 (initial flight) 15.5	20–38.9	>41	Gaylord et al. 2008
<i>Dendroctonus brevicomis</i>	18.6 (initial flight) 13.1	19–38.9	>41	Gaylord et al. 2008
<i>Dendroctonus frontalis</i>	17.8 (initial flight) 15	19–37.9 27	>41 >36.7	Gaylord et al. 2008 Thompson and Moser 1986
<i>Dendroctonus valens</i>	16.1	19–37.9	>41	Gaylord et al. 2008
<i>Dendroctonus adjunctus</i>	14.5 (initial flight) 11.4	14–27.9	38	Gaylord et al. 2008
<i>Dendroctonus approximatus</i>	17.5 (initial flight) 16.3	17–38.9	>41	Gaylord et al. 2008
<i>Dendroctonus ponderosae</i>	16	25–30	>30	Gray et al. 1972
<i>Ips typographus</i>	17.5 16 (initial flight)	22–26		Botterweg 1982 Öhrn et al. 2014 Wermelinger 2004
<i>Hylurgus ligniperda</i>	10.6	13.6–17.5		Mausel et al. 2007
<i>Hylastes ater</i>	11.4	19.9		Mausel et al. 2007

Note: Data have been converted from their original units to units of °C for comparative purposes.

4.1.2. Temperature effects on flight

Abiotic factors are often correlated and act together to affect flight in insects. As beetles are ectotherms, both flight initiation and sustained flight behaviours are dictated by temperature. Flight thresholds vary with bark beetle species, but minimum, maximum, and optimal flight temperatures are known for many species (Table 2). These thresholds can help managers predict when dispersal will occur for different species of bark beetle.

The minimum temperature required for flight initiation in most bark beetles is higher than that required for sustained flight. Once beetles begin to fly, they can maintain flight even at temperatures below optimal levels (Atkins 1961; Gaylord et al. 2008). For example, *D. pseudotsugae* initiate flight when temperatures reach 17.8 °C; however, flight is sustained if temperatures subsequently drop to as low as 6.7 °C (Atkins 1961). *Dendroctonus pseudotsugae* is the only known species for which the duration of initial flight is impacted by temperature. The duration of the initial flight almost doubled when temperatures increased from 20 to 32 °C (Atkins 1961). In addition, flight continuity of *D. pseudotsugae* increases with temperature within this range (Atkins 1961). *Dendroctonus pseudotsugae* is not able to initiate flight at temperatures below 18–20 °C but can conduct sustained flight at 13 °C (Rudinsky and Vite 1956). Flight duration of *D. pseudotsugae* is similar at temperatures between 17 and 32 °C. This may be because wing-beat frequency increases with temperature only until the beetle takes off in the initiation of flight (Atkins 1960). Emergence from the natal host and flight activity is dictated by temperature in *D. ponderosae*, with flight initiated at 16 °C (McCambridge 1971). Spontaneous flight of *D. ponderosae* occurs between 22 and 32 °C (Shepherd 1966). The optimum flight temperature is higher for *Ips confusus* that is found in warm habitats in southwestern North America. The threshold for flight initiation by *I. confusus* occurs at 25 °C, but optimum temperatures for takeoff are somewhat higher and differ by sex (Borden 1967). Some field studies illustrate the importance of temperature to bark beetle dispersal by flight. There is a direct relationship between the number of *D. rufipennis* captured

in pheromone-baited traps and the accumulation of degree hours above the flight threshold of 13.3 °C (Safranyik and Linton 1987).

In addition to minimum temperature flight thresholds, maximum temperatures also dictate bark beetle flight. In a study of three *Ips* species and five *Dendroctonus* species in ponderosa pine forests in the southwestern US, maximum daily temperature was more important in predicting bark beetle flight activity than minimum flight temperature (Gaylord et al. 2008). Flight activity is disrupted at temperatures above maximum thresholds but will resume as temperatures lower into the optimal range. For example, *D. approximatus* arrest flight at temperatures above 41 °C (Gaylord et al. 2008). Flight by *D. ponderosae* is limited at temperatures above 30 °C (Gray et al. 1972), severely restricted above 38 °C, and completely inhibited above 41 °C (McCambridge 1971).

Temperature might also affect bark beetle flight through an indirect effect on the energy reserves used in flight. High bark temperatures result in the emergence of low-quality *D. ponderosae* individuals (Chubaty et al. 2014), and this might reduce the energy available for flight (Evenden et al. 2014). Individual energy level can influence host selection decisions (Atkins 1966) of *D. ponderosae*, as beetles with high energy reserves are more host-selective than those with low energy reserves, which accept poor-quality trees (Chubaty et al. 2009; Latty and Reid 2010). In laboratory studies, *D. ponderosae* held at 5 °C for 24 h prior to flight have a marginally longer sustained flying time than beetles held at 24 °C before the flight assay (Wijerathna 2016).

4.1.3. Humidity

The impact of humidity on bark beetle flight has been less well studied than temperature, and these two factors are inextricably linked. Response to humidity is variable in different bark beetle species. Humidity negatively impacts takeoff and initial flight dispersal in *I. typographus* such that approximately half as many beetles fly at 71% relative humidity (RH) compared with 49% RH (Franklin and Grégoire 1999). In contrast, the duration and velocity of the initial flight of *D. pseudotsugae* increases with RH, but

total flight duration is not impacted by humidity (Atkins 1961). When temperatures are below the threshold required for flight, higher RH increases the wing-beat frequency of *D. pseudotsugae* (Atkins 1960). At optimal flight temperatures, however, humidity has little impact on wing-beat frequency (Atkins 1960). More research on the impact of humidity on bark beetle flight is needed, especially the potential interaction between humidity and temperature on flight propensity and capacity.

4.1.4. Effect of wind on short-distance dispersal

Wind speed and direction can have a large impact on the flight of small insects such as bark beetles. Wind can influence the distance that bark beetles fly, the energy used during flight (Jackson et al. 2008), and the direction in which beetles disperse (Byers 2004). The average dispersal distance of most bark beetles is less than 5 km (Kinn 1986; Williams and Robertson 2008; Evenden et al. 2014), and wind direction and speed can impact beetle flight capacity and dispersal within the tree canopy. *Ips sexdentatus* dispersal is greater in the downwind direction at wind speeds that exceed 3 m·s⁻¹ (Jactel 1991). The majority of individuals caught in upwind traps are located within 100 m of the release site, whereas downwind dispersers reach 600 m from the release site (Jactel 1991). At low wind speeds, dispersal direction of *D. ponderosae* is not influenced by wind direction (Safranyik et al. 1989). *Ips pini* and *Scolytus multi-striatus* (Marsham) arrest all flight at wind speeds of 4.8 and 5 km·h⁻¹, respectively (Seybert and Gara 1970; Meyer and Norris 1973). *Dendroctonus frontalis* are unable to fly at wind speeds above 2 m·s⁻¹ (Coster and Gara 1968). In a laboratory wind tunnel study, *D. ponderosae* flew for longer at 0, 0.5, and 1 m·s⁻¹ than when exposed to wind of 2 m·s⁻¹ (Wijerathna 2016).

Wind speed can influence energy utilization by bark beetles during dispersal. Beetles undergoing passive transport use less energy than those that actively fly below the canopy layer, which allows them to disperse for longer periods of time (Jackson et al. 2008). *Dendroctonus ponderosae* and *I. typographus* mostly disperse in the downwind direction, so as not to expend unnecessary energy (Safranyik et al. 1989, 1992; Byers 2004). There is a positive relationship between wind speed and the number of *I. pini* and *S. multi-striatus* that fly downwind (Seybert and Gara 1970; Meyer and Norris 1973). Wind interacts with beetle physiological state to influence flight direction in *H. ligniperda*. Flight-naïve beetles fly with the wind and are caught in downwind-positioned traps, whereas the direction of dispersal is not influenced by wind in flight-experienced individuals (Meurisse and Pawson 2017).

4.1.5. Wind-aided long-distance dispersal

Beetles have the potential to disperse over hundreds of kilometres when flight is aided by wind (Safranyik et al. 2010). For example, *Dendroctonus ponderosae* can move 30 to 110 km per day in above-canopy flight aided by the wind (Jackson et al. 2008). Dispersal above the canopy occurs in several bark beetle species, including members of the genera *Ips* (Forsse and Solbreck 1985; Jactel 1993), *Dendroctonus* (Jackson et al. 2008), and *Scolytus* (Furniss and Furniss 1972).

Dispersal above the canopy can propel bark beetles across large geographic barriers to establish populations in novel locations (de la Giroday et al. 2011). This type of dispersal promoted the recent range expansion of *D. ponderosae* east of the Rocky Mountains (Safranyik et al. 2010). Aeolian movement promoted landscape-level dispersal of *D. ponderosae* that resulted in range expansion to the north (de la Giroday et al. 2012), south, and east (Cerezke 1981). Landscape-level features may act as conduits for dispersal of *D. ponderosae* as south-facing ridges, canyons, and valleys are infested following long-distance dispersal events (de la Giroday et al. 2011). Directional wind movements result in *D. ponderosae* infestations on the windward sides of geographic barriers (de la Giroday et al. 2011). Due to the strong directionality of wind, beetles undergoing aeolian movement may end up in unsuitable habitats. The recov-

ery of a number of *Ips*, *Dendroctonus*, and *Scolytus* beetles in snowfields, 1.2 km above the timberline, is likely due to deposition of beetles after long-distance dispersal on the wind (Furniss and Furniss 1972).

4.1.6. Light

Light radiation also influences insect flight, and effects of light and temperature are often confounded in nature (Johnson 1969). Most species of bark beetle are positively phototactic and initiate flight in the presence of light (Botterweg 1982). Laboratory experiments on *S. multi-striatus* show a positive phototactic response during flight that exceeds the geotactic response of the beetle (Choudhury and Kennedy 1980). *Dendroctonus ponderosae* are photopositive upon emergence from the natal host; however, at temperatures above 35 °C, *D. ponderosae* become negatively phototactic (Shepherd 1966).

The flight distance of *D. armandi* varies with light quality. Flight distance is greater under artificial illumination than in natural light and dark conditions (Chen et al. 2010). Similarly, *D. ponderosae* have only negligible flight in the dark (Wijerathna 2016). Wing-beat frequency of *D. frontalis* increases with light intensity (Atkins 1960). In addition to a phototactic response, bark beetles regulate flight activity with respect to photoperiod. *Pityophthorus juglandis* (Blackman) fly at dusk, with the highest flight activity occurring between 1800 and 2000 h (Seybold et al. 2012). This may be an adaptation to daily temperature fluctuations. During periods of extremely high temperatures, *P. juglandis* exhibit a bimodal flight pattern at dawn and dusk (Seybold et al. 2012). Photoperiod is the major factor that determines flight activity of *I. typographus*, while other environmental factors only secondarily affect flight. Swarming behaviour of *I. typographus* occurs in response to sunshine (Wermelinger 2004). *Dendroctonus ponderosae* fly for longer periods and greater distances with increasing day length when temperature is held constant (Wijerathna 2016). These increased flight distances could have implications for beetle dispersal at northern latitudes within the expanded range of this species (Wijerathna 2016).

4.1.7. Evaluation of abiotic factors on flight

As bark beetles are ectotherms, environmental abiotic factors have a large influence on insect flight. Abiotic factors are often correlated and act together to dictate both flight initiation and sustained flight. Flight research on bark beetles indicates that both temperature and wind play large roles in dispersal. Temperature dictates the initiation and timing of flight. Many bark beetles are constrained to initiate flight in a small range of optimal flight temperatures, and flight initiation outside of this optimal range can detrimentally affect beetle dispersal success. Wind dictates both the direction and distance of flight. As small-bodied insects, bark beetles rely on strong wind currents for long-distance dispersal. Bark beetles cannot cross large geographic barriers without the help of wind currents. The influence of the abiotic environment on insect flight is well studied in general, but we have yet to fully understand how interactions between specific abiotic factors such as temperature, humidity, and light influence flight in bark beetles. Understanding the interactions between these factors will help to predict landscape-level movement in these species.

4.2. Biotic factors

4.2.1. Tree density

The density of trees within a stand affects flight of some bark beetle species. It is difficult to tease apart the impact of host density on semiochemical response and flight, but capture of a variety of North American bark beetles in non-baited, passive traps is higher in thinned stands than in non-thinned stands (Safranyik et al. 2004). Based on capture of beetles in pheromone-baited traps, there is a positive relationship between pine tree

host density and capture of *H. ligniperda*, but most *H. ater* were captured at intermediate host density (Chase et al. 2017). Similarly, more *D. ponderosae* were caught using passive traps in dense stands compared with thin stands, but trees with the highest attack density were those in thin stands (Negrón 2019). Beetle diversity is highest at intermediate levels of canopy cover in trapping experiments conducted in Norway spruce stands (Zach et al. 2010). According to computer models, *D. ponderosae* spread is actually greatest through forests with low tree density (Powell et al. 2018). Robertson et al. (2007) note, however, that *D. ponderosae* dispersal is greatest in dense stands of high-quality hosts, if weather conditions are ideal. Newly emerged beetles are less likely to leave the natal stand when host tree density is high (Powell and Bentz 2014). Trapping of *D. ponderosae*, *I. typographus*, and *I. pini* shows that more beetles accumulate at the edges of intact stands (Reid 2008; Kautz et al. 2013).

4.2.2. Symbiotic organisms

Bark beetles are associated with a large number of both beneficial and harmful symbiotic organisms. These symbioses can range from beneficial to parasitic and may impact the flight capacity of the beetle host. Infections by endoparasitic nematodes change flight behaviour in *I. paraconfusus*, as flight distance decreases with infection level (Hagen and Atkins 1975). This relationship may be driven by lower lipid levels in individuals with high nematode infections (Hagen and Atkins 1975). Nematode infection, however, shows no impact on flight behaviour of *I. typographus* (Forsse 1987). Infection results in reduced protein levels in *I. sexdentatus* measured after flight swarming behaviour (Lieutier 1984). Nematode infection in *D. pseudotsugae* negatively impacts only initial flight and does not impact total flight duration or wing-beat frequency (Atkins 1960, 1961). Nematodes reside on the wings of *D. rufipennis*; however, the greatest nematode load occurs on overwintering beetles, and fewer nematodes are found on beetles before and after flight (Cardoza et al. 2006).

Phoretic mites are frequently found in association with bark beetles (Moser and Roton 1971; Rodrigueiro and Do Prado 2004; Cardoza et al. 2008; Grossman and Smith 2008; Mori et al. 2011). Phoretic relationships may be commensalistic or mutualistic and, in some cases, can negatively impact the host beetle (Hofstetter et al. 2006). Mite load influences flight capacity of *D. frontalis* as beetles captured low in the canopy are more heavily infested than beetles captured high in the canopy (Kinn and Witcosky 1978). Clusters of mites at the tips of the elytra of *D. pseudotsugae* significantly reduce wing-beat frequency and, presumably, flight capacity (Atkins 1960).

4.2.3. Population dynamics and density

There is a large degree of variation in flight performance within populations of bark beetles (Forsse and Solbreck 1985; Salom and McLean 1991; Jactel and Gaillard 1991; Evenden et al. 2014). Bark beetle flight phenotypes within a population can range from non-flyers to beetles that exhibit exceptionally long flights (Evenden et al. 2014) that can extend over 50 km (Jactel and Gaillard 1991).

Intraspecific variation in physiology drives differential dispersal, which promotes an evolutionarily stable dispersal strategy within populations (Kautz et al. 2016). High within-population variation in flight capacity increases leptokurtic flight distributions and the likelihood of rare dispersal events such as long-distance dispersal (Kautz et al. 2016). A recently developed individual-based model (Kautz et al. 2016) and empirical studies (Latty and Reid 2010) reveal that the variability in flight capacity of individual bark beetles within a population may be retained as a strategy to increase colonization. Resource trade-offs may occur as energy consumption during dispersal flight may reduce energy allocation to pheromone production (Gries et al. 1990), detoxification of tree defenses during host colonization (Reid et al. 2017), mating (Elkin and Reid 2004), and offspring production (Wijerathna et al. 2019), whereas the initia-

tion of host colonization without dispersal and prior to energy expenditure would increase intraspecific resource competition.

This non-uniform movement exhibited by bark beetles is referred to as stratified dispersal and is characterized by long-distance dispersal of a small subset of the population in combination with local spread. Only a small percentage, approximately 2.5%, of the *D. ponderosae* population attempts long-distance dispersal (Safranyik et al. 1992). Stratified dispersal makes modelling and predicting movement difficult, as the population is not moving according to a simple diffusion model, but rather toward a leptokurtic distribution (Liebhold and Tobin 2010). Stratified dispersal can result in small spot infestations far away from the larger source population that, in combination with beetle aggregation, allows for a fast spread rate (Liebhold and Tobin 2010). Dispersal success in resistant habitats, which are characterized by non-hosts or poor-quality hosts, is highest with the greatest variability of dispersal capacity among individuals (Kautz et al. 2016). Reduced variation within the population is only advantageous when hosts are extremely abundant and susceptible to attack. The maintenance of variability in flight phenotypes allows populations to react to changing environmental conditions and increase population stability (Kautz et al. 2016). In this way, bark beetle populations are likely to adapt well to environmental perturbations associated with climate change (Kurz et al. 2008; Bentz et al. 2016).

Certain bark beetle species exhibit different flight behaviour during different population phases. Although comparisons of flight during endemic and epidemic population phases has not been well studied, *D. ponderosae* that emerge in epidemic populations are more likely to attack a new host in close proximity to the natal host. In endemic populations, new attacks do not occur near the natal hosts (Safranyik and Carroll 2006). During epidemic conditions, *D. ponderosae* are less selective of stand quality, which could potentially explain the short dispersal distances before host selection during outbreaks (Robertson et al. 2007). Large windthrow events can be the driver of *Ips typographus* population outbreaks (Potterf and Bone 2017). Unlike *D. ponderosae*, *I. typographus* from endemic populations exhibit short but highly variable flight distances. Once a windthrow event occurs, the variation in flight distance decreases and the population transitions to the epidemic population phase in which beetles fly further during the dispersal phase (Potterf and Bone 2017).

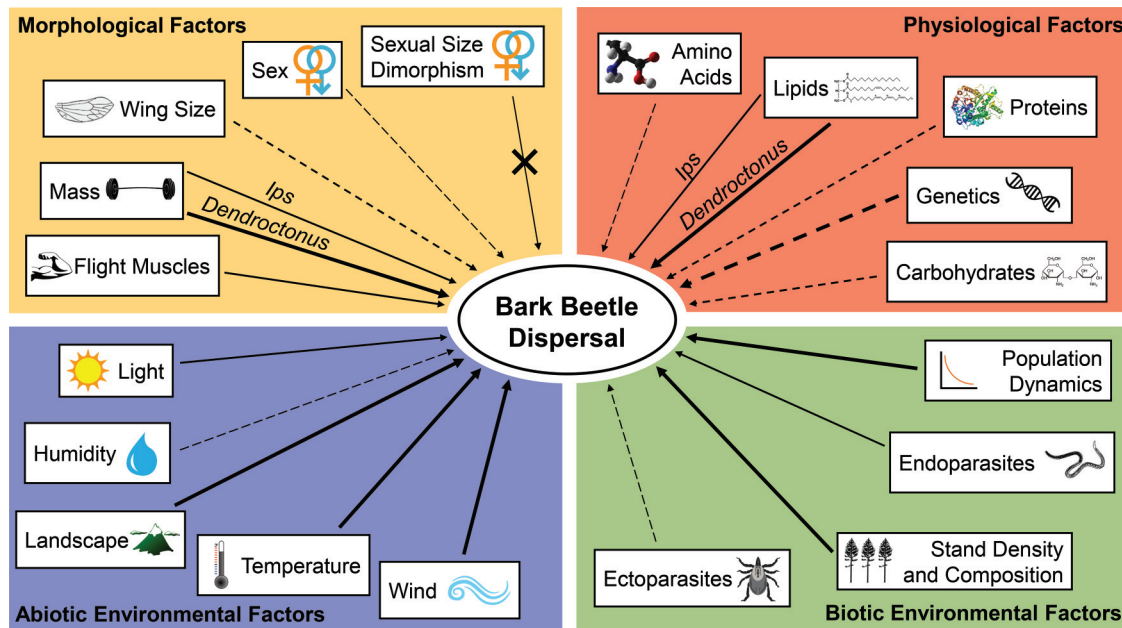
4.2.4. Evaluation of biotic factors on flight

The influence of biotic factors in the environment on bark beetle flight is not well documented in the literature. Bark beetle symbionts, both beneficial and detrimental, can alter beetle flight capacity through increased wing loading or infection effects on beetle health. Tree density probably influences dispersal by weak fliers, as dispersal through dense stands requires maneuvering around physical barriers. Although directed flight to semiochemical cues is well studied in bark beetles, the influence of perception of semiochemicals on flight capacity in general has received little attention. It is possible that the interaction between beetle physiological state and responsiveness to semiochemicals drives dispersal distance before host colonization in bark beetles. Population phase will also likely interact with beetle physiological state to influence bark beetle dispersal. Future research should focus on understanding how flight behaviour changes with population phase, especially in outbreaking species.

5. Discussion

Dispersal by flight is a key part of the life cycle of bark beetles; it is an obligatory phase that occurs from the natal host to a new reproductive host. As bark beetles are both ecologically and economically important, an understanding of this crucial life history trait is important to predict spread and manage tree-killing bark beetle species. In this review, we examine the various morpholog-

Fig. 3. Relative importance of factors that influence bark beetle flight. The thickness of each line indicates the importance of the factor on dispersal by flight. The thinnest lines indicate that there is an effect of the factor on flight, but not a strong effect. The thickest lines indicate the factors that have the strongest influence on flight and have been studied in multiple species. The solid lines indicate that much research has been conducted and we have a good understanding of how the factor influences flight. The dashed lines indicate that not much research has been conducted on the factor. Dashed lines also vary in thickness, with the thickest dashed lines indicating the most promising factors that should be further explored in future research. An “x” through a line means that there is little to no effect of the factor on flight. A box with two lines indicates that the factor varies in importance across bark beetle genera. All images are publically available through the Creative Commons (CC0) Public Domain license. [Colour online.]



ical, physiological, biotic, and abiotic factors that influence scolytid dispersal.

The relative importance of these factors in affecting intra- and inter-species variation of flight response are compared (Fig. 3). From this synthesis, we conclude that the most important factors that influence dispersal by flight are (i) beetle body mass, (ii) lipid content, (iii) external temperature, (iv) wind, (v) landscape characteristics, and (vi) stand density and composition (Fig. 3). Although the directionality and significance of these influential factors will be different among species and genera of bark beetles, these are the main factors that should be considered when developing models for bark beetle flight. In addition to these important factors that are known to influence dispersal, we also highlight genetic studies on dispersal that show promise for explaining within-species flight variation. These and many other factors can influence dispersal of bark beetles on the landscape. Future studies need to determine how interactions among factors influence flight and incorporate these interactive effects into modelling efforts.

Detailed research on the factors impacting bark beetle flight can describe a more accurate dispersal kernel model to predict movement and aid in the management of future outbreaks. This process would begin with the derivation of a mechanistic or phenomenological model for dispersal distance based on the most important dispersal factors. Once the model is developed, one can use maximum likelihood estimation to find the parameter values that best fit the model given the empirical data (Clark 1998). The tails of the dispersal kernel are extremely important for calculating population spread rates. The primary difficulty in fitting dispersal kernel models to data, however, is in estimating the tail due to lack of data in the region of study. Flight mill data prove extremely valuable for the estimation of this tail, as mills record the behaviour of both non-fliers and long-distance fliers, which

depicts the various flight phenotypes and relative flight capabilities across entire populations.

The use of fat-tailed dispersal kernels to model population spread has been widely discussed in the literature. They are commonly used to model populations with long-distance dispersal events (Clark 1998; Rieux et al. 2014; Saura et al. 2014). It is known that fat-tailed dispersal kernels can lead to accelerated spread rates (Kot et al. 1996), although such kernels should generally be truncated at some upper bound that reflects the plausible upper biological limit of dispersal capacity (Kot et al. 1996). Long-distance dispersal events of bark beetles cannot be ignored as they permit movement across geographic barriers and range expansion (Furniss and Furniss 1972; Jackson et al. 2008). For fat-tailed dispersal kernels to predict movement, however, information on the proportion of the population that undergoes long-distance dispersal and the upper limits of this dispersal are needed.

The process of developing a dispersal kernel is complex and is dependent on the question at hand and the important factors that one wants to include in the model. If the only interest is having a model for predicting dispersal, then using a phenomenological approach to simply fit dispersal data to a dispersal kernel with a given functional form is sufficient. If the question of interest, however, is the degree to which different factors influence dispersal, then the process becomes more involved and a mechanistic modelling approach is needed. A mechanistic model is derived from first principles and provides insight into the individual mechanisms and how they relate to dispersal. Nathan et al. (2012) provide a detailed review on how to fit dispersal kernels to data.

Models, including dispersal kernels, help us to understand key components in bark beetle population spread such as population establishment, the rate of spread, and species interactions. Forest managers are commonly faced with difficult decisions on how to control invasive species and understand how a newly invasive

species will perform in a new environment in the short and long terms (Hastings et al. 2005). The insight from modelling efforts can help managers answer important questions concerning species establishment, spread, and control efforts. In particular, the minimum population level needed for persistence of a newly introduced species can be calculated (Goodsman and Lewis 2016) to determine if a newly introduced species can outcompete native species and persist in the new environment (Hart and Gardner 1997). If the species does become established, models can be used to predict how fast the population will spread (Kot et al. 1996).

Further development of robust predictive models for bark beetle dispersal requires greater integration with the multiple factors that influence dispersal, including those that we review here (Fig. 3). Future improvement of modelling bark beetle spread should focus on developing mechanistic dispersal models that include parameterization with data on beetle physiology, morphology, genetics, and the role of the abiotic and biotic environments (Fig. 3). Models become especially important in the face of climate change, where changing environmental conditions can induce extreme outbreak conditions in certain species of tree-killing bark beetles (Safranyik et al. 2010). These models will need to be flexible to incorporate these future abiotic conditions. Such models will be essential for forecasting future spatial and temporal dynamics of economically important bark beetle pests with expanding ranges. Accurate predictive models for bark beetle dispersal in combination with climate change models can help determine future movement and risk of economically important bark beetle pests.

Acknowledgements

This research was supported by a grant to from the Natural Sciences and Engineering Research Council of Canada (grant no. NET GP 434810-12) to the TRIA Network, with contributions from Alberta Agriculture and Forestry, fRI Research, Manitoba Conservation and Water Stewardship, Natural Resources Canada – Canadian Forest Service, Northwest Territories Environment and Natural Resources, Ontario Ministry of Natural Resources and Forestry, Saskatchewan Ministry of Environment, West Fraser, and Weyerhaeuser (Maya Evenden).

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