Ecología Austral 27:305-311 Agosto 2017
Asociación Argentina de Ecología
https://doi.org/10.25260/EA.17.27.2.0.478

Firewood as a pathway for insect introductions. What are the risks of ant invasions in Patagonia?

Victoria Werenkraut[1,✉]; Gabriela I. Pirk[1]; María N. Lescano[1]; José D. Benclowicz[2] & Luciana Elizalde[1]

[1] *INIBIOMA, UNCOMA, CONICET, Laboratorio Ecotono, Centro Regional Universitario Bariloche, (8400) Bariloche, Río Negro, Argentina.* [2] *IIDYPCA, UNRN, CONICET, (8400) Bariloche, Río Negro, Argentina.*

Abstract. Firewood can act as a long-distance dispersal vector for wood-infesting insects both within and among countries. Recently, we detected the alien carpenter ant *Camponotus mus* in firewood transported from central Argentina to Patagonia. This species generates significant economic losses in its native range and has invader potential. Moreover, global warming and the increasing anthropogenic disturbance in Patagonian ecosystems make them highly susceptible to insect invasions. This is especially alarming considering the current lack of sanitary controls of incoming goods into the region. To prevent insect introductions via firewood, it is crucial to implement a joint effort among the scientific community, control organisms, government and end user.

[Keywords: alien species; *Camponotus mus*; long-distance dispersal; non-native species; social insects]

Resumen. La leña como vía para la introducción de insectos. ¿Cuáles son los riesgos de las invasiones de hormigas en la Patagonia?. La leña puede actuar como vector de dispersión de insectos a larga distancia, tanto dentro como entre países. Recientemente encontramos en Patagonia a la hormiga carpintera exótica *Camponotus mus* en leña transportada desde el centro de la Argentina. Esta especie tiene potencial invasor, y en su rango nativo genera pérdidas económicas significativas. Además, el calentamiento global y el incremento de los disturbios antrópicos en los ecosistemas Patagónicos los vuelven muy susceptible a las invasiones de insectos. Esto es especialmente alarmante dada la falta de controles sanitarios en el transporte de bienes hacia la región. Para prevenir introducciones de insectos a través de la leña es necesario un esfuerzo conjunto de la comunidad científica, los organismos de control, el gobierno y los usuarios finales.

[Palabras clave: especies exóticas, *Camponotus mus*, dispersión a larga distancia, especies no nativas, insectos sociales]

Introduction

Historically, geographical barriers such as oceans and mountain ranges limited species dispersal, but these barriers have been overcome by human activities (Liebhold et al. 1995). Nowadays, human movements and trade facilitate the mid and long-distance dispersal of many species (e.g., Suárez et al. 2001; von der Lippe and Kowarik 2007), which allows the first and last stages underlying biological invasions: arrival (transport of individuals to new areas outside their native range) and spread (expansion of invading species' geographical range in invaded areas) (Shigesada and Kawasaki 1997). Indeed, there is a positive relationship between the relative abundance of invasive species in different countries and the volume of trade (Vila and Pujadas 2001; Westphal et al. 2008).

Many species are unintentionally transported as the byproduct of the movement of goods. The transport of raw and processed wood products like logs, firewood, timber, lumber, and wood packaging materials has been responsible for the dispersal of many insects from different orders (e.g., Roques and Auger-Rozenberg 2006; Jacobi et al. 2012). Special attention has been paid to the arrival and spread of bark and wood-boring insects that represent serious ecological and economic threats to forests health (e.g., Smith et al. 2004; Muirhead et al. 2006; Boissin et al. 2012). Wood products can also harbor social insects (Ormsby 2003; Suárez et al. 2005), and although they do not represent a direct risk for native and non-native forest health, their arrival in new areas may have impacts on biodiversity and/or cause sanitary problems in urban and peri-urban areas (MacDonald et al. 1980; Ormsby 2003).

Among wood products, firewood is a common pathway by which wood-infesting insects can spread both within and among

Editora asociada: Roxana Aragón

✉ vicwkt@gmail.com

Recibido: 18 de noviembre de 2016
Aceptado: 31 de marzo de 2017

countries (Haack et al. 2010; Koch et al. 2012), giving way to important insect pests (Muirhead et al. 2006; Cameron et al. 2008). For instance, the Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky, Coleoptera: Cerambycidae) and the emerald ash borer (*Agrilus planipennis* Fairmaire, Coleoptera: Buprestidae) are serious economic and ecological threats to North American and Canadian forests. Both beetle species tend to travel fewer than two kilometers on their own, but have infested new areas by human-assisted transportation with firewood and nursery stock as a vector (Poland et al. 1998; Crocker et al. 2007; Kovacs et al. 2010). *Agrilus coxalis* Waterhouse (Coleoptera: Buprestidae) is a boring species native to Guatemala, Mexico and Arizona and has been linked to widespread oak (*Quercus* spp. L.) mortality in southern California (Coleman and Seybold 2008). Here again, firewood transport has been suspected in the spread of *A. coxalis* from either Arizona or northern Mexico to California (Coleman and Seybold 2008). In a recent US survey of firewood retailers, live insects emerged from almost 50% of around 400 firewood bundles analyzed (Jacobi et al. 2012). This is not surprising as firewood is commonly cut from stressed, dying or recently dead trees, which often harbor various insects and diseases (Hanks 1999; Lieutier et al. 2004). Thus, long distance firewood movement represents a risk for forest health and also for biodiversity, human health and economy.

Although it could be a potential danger, firewood movement risk has not been studied in Patagonia. We have recently detected *Camponotus mus* Roger (Hymenoptera: Formicidae) living individuals in firewood (*Prosopis torquata* (Cav. ex Lag.) D.C.) transported from central Argentina, purchased in Bariloche (Patagonia, Argentina), at about 500 km beyond its native range. The discovery was made before the onset of southern summer. Around 20% of the logs harbored more than 100 individuals of *C. mus*, including immature stages. Individuals in isolated logs kept indoors survived more than five months. During the summer and autumn we kept on finding *C. mus* individuals, along with other arthropods, in firewood purchased at the same retailer. Here we discuss: a) the status of ants in general, and of *Camponotus* genus in particular, as potential invaders; b) the suitability of Patagonia to ant invasions, and c) the current regulations and controls on firewood transport in Patagonia. Finally, we provide some future directions with the aim of preventing the introduction of these and other insects transported in firewood to Patagonia which can be applied to potential introductions worldwide.

Ant introductions

Several social insects' traits facilitate their invasive success. Their generalist diet and social lifestyle provide individual and colony-level responses, enabling them to adjust to conditions in the new area (Rust and Su 2012; Ugelvig and Cremer 2012). Invasive ants are generally omnivorous and build superficial and/or ephemeral nests allowing them to move fast and colonize new sites when the environment becomes unsuitable. They may form supercolonies with workers that lack aggressive behaviors among different nests, or at least have many fertilized queens, conferring them a reproductive advantage (Holway et al. 2002). There are around 200 ant species (1.6% of all ant species) that have successfully established outside their native ranges around the world (McGlynn 1999). Five of them are among the world's 100 worst invasive species (Lowe et al. 2000). Also, species with apparently no effects on invaded ranges could still pose serious threats in the long term since impacts are often detected long after their arrival (Suárez et al. 2005). Many more regularly transported species could become established in new areas, either invading natural ecosystems or remaining in close association with humans (i.e., "tramp ants") (Holway et al. 2002).

The main impact of invasive ants on ecosystems is the reduction in the diversity and abundance of native ants, leading to direct and indirect effects on other taxa (Holway et al. 2002). They may even disrupt crucial mutualistic interactions among native plants and insects (Holway et al. 2002). In urban areas, introduced ants could become pests and affect human health through their stings or biting, or act as mechanical vectors of pathogenic agents (Robinson 1996; Josens et al. 2014). They can also damage structures, electronic devices and affect household residents (Bueno 1997). Thus, ant introductions may have ecological and human-related impacts.

Ant introductions have occurred as a consequence of human trade (Holway et al. 2002). Ants may arrive in different kinds of transported goods (Suárez et al. 2005; Ward

et al. 2006). In the US, 12% of arriving species established successfully and the probability of establishment increased with the number of times a species was transported (Suárez et al. 2005). Either complete or fragmented colonies may arrive in transported vectors. Since solitary queens may not bear enough metabolic reserves to found colonies (Hee et al. 2000), the presence and number of workers is a determinant of colony survival (Holway el al. 2002).

The genus *Camponotus* is one of the most specious and widely distributed ant genus of the world (Akre et al. 1995). Several *Camponotus* species, also known as carpenter ants, are important pests in urban areas (Della Lucia 2003; Chacón de Ulloa 2003), and at least one has been recorded as invasive (*C. planatus* Roger; Suárez et al. 2005). This genus was the fifth most frequently intercepted one at the New Zealand border (Ward et al. 2006), suggesting its potential of being introduced and becoming established. Some carpenter ants can dig into wood to build their nests. In North America, about 23 species are structural pests, and seven cause severe damage to wooden structures, generating multi-million-dollar losses (Akre et al. 1995).

In South America, *C. mus* has several invasive traits (Holway et al. 2002; Krushelnycky et al. 2010). It dominates its communities, it is omnivorous, and use aphids' honeydew as an important source of carbohydrates. This species has great behavioral and physiological plasticity, reflected in its wide geographical distribution: arid and humid areas in north and central Argentina, southern Brazil, Uruguay and part of Paraguay (Kusnezov 1951). *C. mus* may have several gyne per nest (Kusnezov 1951), increasing the chances of colony survival if a fraction of it, with at least one queen, is transported by humans. This species generates significant economic losses in its native range as it nests in all types of buildings, where it can gnaw into structural wood, insulation materials and foundations (Josens, personal communication). In addition, it can nest in electrical equipment, causing short-circuits and damaging engines (Josens, personal communication).

SUSCEPTIBILITY OF PATAGONIA TO ANT INVASIONS

The chance of establishment of an alien species increases markedly with the rate of arrival at the new environment (Kolar and Lodge 2001), but other factors are also important (Lonsdale 1999; Davis et al. 2000). Among abiotic factors, successful establishment has been related to climate change (Dukes and Mooney 1999; Walther et al. 2009) and disturbance, mainly of human origin (Tschinkel 1988; Byers 2002). Among biotic factors, the outcome of the interactions of alien species with native ones is crucial in determining their success (De Rivera et al. 2005).

In Patagonia, a cold-climate region (mean annual temperature ranges from 3 °C to 12 °C, with absolute minimum temperatures lower than -20 °C [Paruelo et al. 1998]), global warming may facilitate the establishment of aliens by providing suitable thermal conditions to allow non-native warm-adapted species to thrive in it, as has been predicted for alien insects on the sub-Antarctic islands (Lebouvier et al. 2011). Warmer temperatures may also cause seasonally stressful conditions for cold-adapted species reducing intraspecific competition and promoting vacant niches. Anthropogenic disturbance influences the vulnerability of an ecosystem to invasion (Lodge 1993; Burke and Grime 1996) and usually favors the establishment of alien ants (King and Tschinkel 2006; Menke and Holway 2006). During the last century, anthropogenic disturbance in Patagonia has increased as a consequence of the concentration of human population (Aizen 2014). The combination of all this may turn Patagonia into a region highly vulnerable to ant invasion.

Resident species reduce the success of alien species (i.e., biotic resistance) (Elton 1958). Invading species are more likely to establish where levels of competition among the resident species are low (Drake et al. 1989; Moller 1996). The Patagonian's susceptibility to successful establishment and spread of alien ants may be influenced by its relatively poor ant species richness (see Kusnezov 1953; Fergnani et al. 2010). The reduced interspecific competition in unsaturated ant communities, especially considering that the worst enemy of an ant is another ant (Forel 1874), may facilitate alien ants to become successful invaders.

In addition, no ant species closely tied to urban areas and human activity has been reported in Patagonia so far. This vacant niche in urban areas combined with the use of firewood for indoor heating may allow aliens to dwell inside houses avoiding the harsh climate. *C. mus*, capable of living in urban environments and nesting in all types

of human constructions, may rapidly occupy this niche unfilled by native ants. Finally, the abundance of wooden constructions (i.e., whole houses, roofs, sheds) in the area would serve as suitable nesting sites for species like *C. mus*.

So far, no studies on ant diversity have been performed in urban areas in north-western Patagonia. In natural areas, *C. mus* has not been recorded (Fergnani et al. 2010; Pirk 2014; Werenkraut et al. 2015). A thermal barrier may be the reason for the absence of this species at these high latitudes. However, in its native range, *C. mus* avoids activity at the warmest hours of the day (Aranda-Rickert and Fracchia 2012) so minimum temperature requirements may not be so restrictive. Even if temperature restricts the survival of *C. mus*, temperature increases caused by climate change could moderate this limitation, favoring its future establishment.

Regulations and controls

Camponotus mus detection in firewood in Bariloche is particularly relevant considering the city characteristics. With about 110,000 inhabitants, Bariloche is the most populous city in Río Negro Province, and one of the most important in Patagonia (INDEC 2010). In the last two decades, Bariloche population increased almost 40%, while national population, 23%. Moreover, it is one of the main tourist destinations in the country, with an intense traffic of people and goods in constant and rapid growth since the 1960s (Benclowicz 2012). For many citizens and tourists, the use of firewood for heating is unavoidable, considering the low temperatures (minimum mean annual temperature 2.3 °C) and the widespread lack of access to natural gas network. Additionally, firewood is commonly used for cooking grilled meat ("asado"), a strongly rooted habit throughout the country.

Traditionally, the possible damage to agricultural production caused by the spread of pests through timber transport has been the main subject of concern of national authorities (Boletín Oficial 1963). In 2006, SENASA, National Health and Food Quality Service body, established phytosanitary treatments for quebracho (*Schinopsis* spp.) raw wood transported to Patagonia, and in 2012, created the National Forest Health Program to control pests (Boletín Oficial 2006, 2012). Nevertheless, officials from agencies involved who were interviewed pointed that controls are almost nonexistent.

The care of the environment has been recently installed on public opinion, and reproduction of native forests was regulated (National Law 26331, 2007; Provincial Law 4552, 2010), although not dealing with pests that could affect them, houses or wooden buildings. This risk does not appear as a concern among authorities and officials or society. The lack of public awareness on the question inhibits any preventive action.

Socioeconomic studies on biological invasions indicate that management costs are generally more efficient if applied as early as possible in the process of invasion (e.g., Leung et al. 2002; Saphores and Shogren 2005). Regarding this, it is essential to implement firewood regulations and sanitary controls on goods entering Patagonia from other regions of Argentina or other countries, aimed at avoiding and/or decreasing the rate of alien insects' arrival.

Future directions

Despite firewood transport to Patagonia is unlikely a recent phenomenon, current conditions (i.e., global warming, the increment in anthropogenic disturbance, and the likely increase in firewood demand associated with population growth) may increase the chances of arrival and successful establishment not only for ants but also for other non-native arthropods including pests and pathogens. Recently a strong association between climate change and the establishment of non-native species has been shown in Great Britain (Hulme 2016). This effect was particularly strong for terrestrial arthropods, in part because their long distance dispersal is specially favored with human trade (Hulme 2016). Thus, the arrival of *C. mus* along with other arthropods deserves to continue being studied in order to prevent their possible establishment. In this sense, we call scientific community attention about the need to study firewood use, pathways, and the potential pests and diseases transported to evaluate the magnitude of this problem, crucial for management and control strategies.

A way to diminish firewood movement is to reduce imported firewood consumption, promoting the use of local firewood. In Patagonia, the use of local wood for heating and cooking is a common practice in rural communities, with long standing fuel use

cognition enriched over generations (Cardoso et al. 2015). Local people knowledge combined with scientific research may be used to propose management strategies for local woody plant species. It has been proposed that the most efficient way to protect native forests may be to manage them for wood products (Liebhold et al. 1995).

Monitoring and control policies are needed to prevent the arrival of non-native arthropods and potential pests and diseases via firewood. Raising awareness about the potential risks of firewood transport among end users is also relevant even if their magnitude is under study. It is particularly important to alert through prevention campaigns that storing firewood near or inside the house may be hazardous. Also, if insects are noticed, firewood should be burned as soon as possible or strictly isolated. Individual actions could contribute with government regulations and controls to reduce the chances of insect invasions. Finally, the best way to obtain successful results in the prevention of insect introductions via firewood is through a joint effort among scientific community, control organisms, government and end users.

ACKNOWLEDGMENTS. Tomás Benclowicz curiosity alerted us about the presence of non-native ants. Fabiana Cuezzo helped with ant determination. Officials from SENASA, National Parks, and Forestry Division of the Río Negro Province provided valuable information about regulations and controls. All the authors are research staff members of CONICET.

REFERENCES

Aizen, M. 2014. Introducción. Pages 13-18 *in* E. Raffaele, M. de Torres Curth, C. L. Morales, and T. Kitzberger (eds.). Ecología e Historia Natural de la Patagonia Andina, un cuarto de siglo de investigación en Biogeografía, Ecología y Conservación. Fundación Azara, Buenos Aires.

Akre, R. D., L. D. Hansen, and E. A. Myhre. 1995. Insect Life: My House or Yours? The Biology of Carpenter Ants. American Entomologist **41**:221-226.

Aranda-Rickert, A., and S. Fracchia. 2012. Are subordinate ants the best seed dispersers? Linking dominance hierarchies and seed dispersal ability in myrmecochory interactions. Arthropod-Plant Interactions **6**:297-306.

Benclowicz, J. D. 2012. Migraciones y representaciones populares en una ciudad turística. Notas sobre San Carlos de Bariloche, Argentina. Diálogo Andino **40**:83-96.

Boissin, E., B. Hurley, M. J. Wingfield, R. Vasaitis, J. Stenlid, C. Davis, P. de Groot, R. Ahumada, A. Carnegie, and A. Goldarazena. 2012. Retracing the routes of introduction of invasive species: the case of the Sirex noctilio woodwasp. Molecular Ecology **21**:5728-5744.

Boletín Oficial de la República Argentina. 1963. Decreto-Ley 6704/1963 Artículo 3, 20/08/1963.

Boletín Oficial de la República Argentina. 2006. Resolución 630/2006, SENASA, 18/09/2006.

Boletín Oficial de la República Argentina. 2012. Resolución 332/2012, SENASA, 11/07/2012.

Bueno, O. C. 1997. Formigas urbanas: identifiçao e controle. Biológico (São Paulo) **59**:17-19.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology **77**:776-790.

Byers, J. E. 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos **97**:449-458.

Cameron, R. S., C. Bates, and J. Johnson. 2008. Distribution and spread of laurel wilt disease in Georgia: 2006-08 survey and field observations. Georgia Forestry Commission report. September 2008 Pp. 28.

Cardoso, M., A. Ladio, S. Dutrus, and M. Lozada. 2015. Preference and calorific value of fuelwood species in rural populations in northwestern Patagonia. Biomass and Bioenergy **81**:514-520.

Chacón de Ulloa, P. 2003. Hormigas urbanas. Pp. 351-359 *in* F. Fernández (ed.). Introducción a las hormigas de la región Neotropical. Instituto de investigación de recursos biológicos Alexander von Humboldt, Bogotá.

Coleman, T. W., and S. J. Seybold. 2008. Previously unrecorded damage to oak, Quercus spp., in southern California by the goldspotted oak borer, Agrilus coxalis Waterhouse (Coleoptera: Buprestidae). The Pan-Pacific Entomologist **84**:288-300.

Crocker, S. J., G. J. Brand, and D. C. Little. 2007. Illinois' forest resources, 2005. Resour. Bull. NRS-13. US Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology **88**:528-534.

Della Lucia, T. M. C. 2003. Hormigas de importancia económica en la región Neotropical. Pp. 337-349 *in* F. Fernández (ed.). Introducción a las hormigas de la región Neotropical. Instituto de investigación de recursos biológicos Alexander von Humboldt, Bogotá.

DeRivera, C. E., G. M. Ruiz, A. H. Hines, and P. Jivoff. 2005. Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. Ecology **86**:3364-3376.

Drake, J. A., H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson. 1989. Biological invasions: a global perspective. John Wiley and Sons, New York.

Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? Trends in Ecology and Evolution **14**:135-139.

Elton, C. S. 1958. Ecology of invasions by animals and plants. Methuen, London.

Fergnani, P. N., P. Sackmann, and A. Ruggiero. 2010. Richness-environment relationships in epigaeic ants across the Subantarctic-Patagonian transition zone. Insect Conservation and Diversity **3**:278-290.

Forel, A. 1874. Les fourmis de la Suisse: Systématique, notices anatomiques et physiologiques, architecture, distribution géographique, nouvelles expériences et observations de moeurs. Société Helvétique.

Haack, R. A., T. R. Petrice, and A. C. Wiedenhoeft. 2010. Incidence of bark-and wood-boring insects in firewood: a survey at Michigan's Mackinac Bridge. Journal of Economic Entomology **103**:1682-1692.

Hanks, L. 1999. Influence of the larval host plant on reproductive strategies of cerambycid beetles. Annual review of entomology **44**:483-505.

Hee, J. J., D. A. Holway, A. V. Suárez, and T. J. Case. 2000. Role of propagule size in the success of incipient colonies of the invasive Argentine ant. Conservation Biology **14**:559-563.

Holway, D. A., L. Lach, A. V. Suárez, N. D. Tsutsui, and T. J. Case. 2002. The causes and consequences of ant invasions. Annual review of ecology and systematics **33**:181-233.

Hulme, P. E. 2016. Climate change and biological invasions: evidence, expectations, and response options. Biological Reviews. DOI: http://doi.org/10.1111/brv.12282.

INDEC (Instituto Nacional de Estadísticas y Censos). 2010. Censo Nacional de Población y Vivienda.

Jacobi, W. R., J. G. Hardin, B. A. Goodrich, and C. M. Cleaver. 2012. Retail firewood can transport live tree pests. Journal of Economic Entomology **105**:1645-1658.

Josens, R., F. J. Sola, N. Marchisio, M. A. Di Renzo, and A. Giacometti. 2014. Knowing the enemy: ant behavior and control in a pediatric hospital of Buenos Aires. SpringerPlus **3**:229.

King, J. R., and W. R. Tschinkel. 2006. Experimental evidence that the introduced fire ant, Solenopsis invicta, does not competitively suppress co-occurring ants in a disturbed habitat. Journal of Animal Ecology **75**:1370-1378.

Koch, F. H., D. Yemshanov, R. D. Magarey, and W. D. Smith. 2012. Dispersal of invasive forest insects via recreational firewood: a quantitative analysis. Journal of Economic Entomology **105**:438-450.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution **16**:199-204.

Kovacs, K. F., R. G. Haight, D. G. McCullough, R. J. Mercader, N. W. Siegert, and A. M. Liebhold. 2010. Cost of potential emerald ash borer damage in US communities, 2009-2019. Ecological Economics **69**:569-578.

Krushelnycky, P. D., D. A. Holway, E. G. LeBrun, L. Lach, C. L. Parr, and K. L. Abbott. 2010. Invasion processes and causes of success. Pp. 245-260 *in* L. Lach, C. L. Parr and K. L. Abbott (eds.). Ant Ecology. Oxford University Press, Oxford.

Kusnezov, N. 1951. El género Camponotus en la Argentina (Hymenoptera, Formicidae). Acta Zoológica Lilloana **12**: 183-252.

Kusnezov, N. 1953. Las hormigas en los Parques Nacionales de la Patagonia y los problemas relacionados. Anales del Museo Nahuel Huapi. APN **3**:105-124.

Lebouvier, M., M. Laparie, M. Hulle, A. Marais, Y. Cozic, L. Lalouette, P. Vernon, T. Candresse, Y. Frenot, and D. Renault. 2011. The significance of the sub-Antarctic Kerguelen Islands for the assessment of the vulnerability of native communities to climate change, alien insect invasions and plant viruses. Biological Invasions **13**:1195-1208.

Leung, B., D. M. Lodge, D. Finnoff, J. F. Shogren, M. A. Lewis, and G. Lamberti. 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proceedings of the Royal Society of London B: Biological Sciences **269**:2407-2413.

Liebhold, A. M., W. L. MacDonald, D. Bergdahl, and V. C. Mastro. 1995. Invasion by exotic forest pests: a threat to forest ecosystems. Forest Science **41**:a0001-z0001.

Lieutier, F., K. R. Day, A. Battisti, J. -C. Gregoire, and H. F. Evans. 2004. Bark and wood boring insects in living trees in Europe: a synthesis. Springer.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution **8**:133-137.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology **80**:1522-1536.

Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the world's worst invasive alien species: a selection from the global invasive species database. Invasive Species Specialist Group (ISSG) Auckland.

MacDonald, J. F., R. D. Akre, and R. E. Keyel. 1980. The german yellowjacket (Vespula germanica) problem in the United States (Hymenoptera: Vespidae). Bulletin of the Entomological Society of America **26**:436-444.

McGlynn, T. P. 1999. The worldwide transfer of ants: geographical distribution and ecological invasions. Journal of Biogeography **26**:535-548.

Menke, S. B., and D. A. Holway. 2006. Abiotic factors control invasion by Argentine ants at the community scale. Journal of Animal Ecology **75**:368-376.

Moller, H. 1996. Lessons for invasion theory from social insects. Biological conservation **78**:125-142.

Muirhead, J. R., B. Leung, C. van Overdijk, D. W. Kelly, K. Nandakumar, K. R. Marchant, and H. J. MacIsaac. 2006. Modelling local and long-distance dispersal of invasive emerald ash borer Agrilus planipennis (Coleoptera) in North America. Diversity and Distributions **12**:71-79.

Ormsby, M. 2003. Pest risk analysis: ants on sawn timber imported from the South Pacific region. Ministry of Agriculture and Forestry, New Zealand. Biosecurity, Forest Authority, M. A. F. Biosecurity

Paruelo, J. M., A. Beltrán, E. Jobbágy, O. E. Sala, and R. A. Golluscio. 1998. The climate of Patagonia: general patterns and controls on biotic. Ecol Austral **8**:85-101.

Pirk, G. I. 2014. Did ash fall from Puyehue-Cordón Caulle volcanic complex affect ant abundance and richness in the Patagonian steppe? Ecología Austral **24**: 23-30.

Poland, T. M., R. A. Haack, and T. R. Petrice. 1998. Chicago joins New York in battle with the Asian longhorned beetle. Newsl. Mich. Entomol. Soc **43**:15-17.

Robinson, W. H. 1996. Urban entomology: insect and mite pests in the human environment. Chapman and Hall.

Roques, A., and M. A. Auger-Rozenberg. 2006. Tentative analysis of the interceptions of non-indigenous organisms in Europe during 1995–20041. EPPO Bulletin **36**:490-496.

Rust, M. K., and N. -Y. Su. 2012. Managing social insects of urban importance. Annual Review of Entomology **57**: 355-375.

Saphores, J. -D. M., and J. F. Shogren. 2005. Managing exotic pests under uncertainty: optimal control actions and bioeconomic investigations. Ecological Economics **52**:327-339.

Shigesada, N., and K. Kawasaki. 1997. Biological invasions: theory and practice. Oxford University Press, UK.

Smith, M. T., P. C. Tobin, J. Bancroft, G. Li, and R. Gao. 2004. Dispersal and spatiotemporal dynamics of Asian longhorned beetle (Coleoptera: Cerambycidae) in China. Environmental Entomology **33**:435-442.

Suárez, A. V., D. A. Holway, and T. J. Case. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. Proceedings of the National Academy of Sciences **98**:1095-1100.

Suárez, A. V., D. A. Holway, and P. S. Ward. 2005. The role of opportunity in the unintentional introduction of nonnative ants. Proceedings of the National Academy of Sciences of the United States of America **102**:17032-17035.

Tschinkel, W. R. 1988. Distribution of the fire ants Solenopsis invicta and S. geminata (Hymenoptera: Formicidae) in northern Florida in relation to habitat and disturbance. Annals of the Entomological Society of America **81**:76-81.

Ugelvig, L. V., and S. Cremer. 2012. Effects of social immunity and unicoloniality on host-parasite interactions in invasive insect societies. Functional Ecology **26**:1300-1312.

Vila, M., and J. Pujadas. 2001. Land-use and socio-economic correlates of plant invasions in European and North African countries. Biological conservation **100**:397-401.

Von der Lippe, M., and I. Kowarik. 2007. Long-Distance Dispersal of Plants by Vehicles as a Driver of Plant Invasions. Conservation Biology **21**:986-996.

Walther, G. -R., A. Roques, P. E. Hulme, M. T. Sykes, P. Pyšek, I. Kühn, M. Zobel, S. Bacher, Z. Botta-Dukát, and H. Bugmann. 2009. Alien species in a warmer world: risks and opportunities. Trends in Ecology and Evolution **24**: 686-693.

Ward, D. F., J. R. Beggs, M. N. Clout, R. J. Harris, and S. O'Connor. 2006. The diversity and origin of exotic ants arriving in New Zealand via human-mediated dispersal. Diversity and Distributions **12**:601-609.

Werenkraut, V., Fergnani, P. N., and A. Ruggiero. 2015. Ants at the edge: a sharp forest-steppe boundary influences the taxonomic and functional organization of ant species assemblages along elevational gradients in northwestern Patagonia (Argentina). Biodiversity and Conservation **24**: 287-308.

Westphal, M. I., M. Browne, K. MacKinnon, and I. Noble. 2008. The link between international trade and the global distribution of invasive alien species. Biological Invasions **10**:391-398.