Arrival rate of nonindigenous insect species into the United States through foreign trade

Timothy T. Work^{1,*}, Deborah G. McCullough², Joseph F. Cavey³ & Ronald Komsa³ ¹Faculté des Sciences, Université du Québec à Montréal, Case Postale 8888, Succursale Centre-Ville, Montréal, Québec, Canada H3C 3P8; ²Department of Entomology and Department of Forestry, 243 Natural Science, Michigan State University, East Lansing, MI 48824-1115, USA; ³USDA, Animal and Plant Health Inspection Service, Plant Protection and Quarantine, 4700 River Road, Unit 133, Riverdale, MD 20737-1236, USA; *Author for correspondence (e-mail: work.timothy@uqam.ca)

Received 16 April 2003; accepted in revised form 1 June 2004

Key words: arrival rates, exotic insects, foreign trade, invasion, globalization, nonindigenous, pathways, plant pests

Abstract

Introductions of invasive nonindigenous species, and the ensuing negative ecological and economic consequences, have increased with expanding global trade. Quantifying the influx of nonindigenous plant pest species through foreign trade is required for national and international risk assessments, monitoring and conservation efforts, and evaluation of ecological factors that affect invasion success. Here we use statistically robust data collected at US ports of entry and border crossings to estimate arrival rates of nonindigenous insect species *via* four cargo pathways and to evaluate the effectiveness of current efforts to monitor arrival of nonindigenous insect species. Interception rates were highest in refrigerated maritime cargo where a new insect species was intercepted on average every 54 inspections. Projected estimates of insect species richness stabilized only for non-refrigerated maritime cargo and US–Mexico border cargo, where inspectors likely detected 19–28% and 30–50% of the species being transported through these respective pathways. Conservative estimates of establishment suggest that 42 insect species may have become established through these four pathways between 1997 and 2001.

Introduction

Invasive species threaten native biodiversity (Vitousek et al. 1997), disrupt ecological processes (Vitousek et al. 1996; Mack et al. 2000), and cause significant economic loss (Pimentel et al. 2000). Many detrimental nonindigenous organisms have been accidentally introduced through commercial foreign trade (Sailer 1978; Calcott and Collins 1996; Niemelä and Mattson 1996) and newly established exotic pests continue to be discovered (Nowak et al. 2001). The frequency of these introductions through commercial trade pathways, and the subsequent potential for establishment and spread has increased with expanding international trade and globalization (US Congress 1993). Sound estimates of the arrival rates of nonindigenous species are required to develop accurate risk assessments for specific pathways or commodities (Byers et al. 2002). Information related to the arrival and diversity of species transported in different pathways is also necessary to develop effective detection or mitigation measures to reduce risks that nonindigenous species will establish and become invasive (National Research Council 2001). Unfortunately, even general information regarding the arrival rate of nonindigenous plant pest species has been largely limited to rules of thumb derived from invasive plants (Shea and Chesson 2002). With the exception of exotic aquatic organisms associated with ballast water (Hallegraeff and Bolch 1992; Carlton and Geller 1993; Locke et al. 1993; Galil and Hulsmann 1997; Pierce et al. 1997; Hulsmann and Galil 2001; Gollasch 2002; Leppakoski et al. 2002), there have been few opportunities to quantify arrival rates of nonindigenous species within specific pathways of invasion associated with cargo and foreign trade (Williamson 1996; Shea and Chesson 2002).

Since 1972, the US Department of Agriculture Animal Plant and Health Inspection Service (USDA-APHIS) has inspected cargo and baggage arriving at US ports-of-entry and border crossings as part of an effort to mitigate risks of nonindigenous plant pest establishment. Inspectors examine up to 2% of cargo arriving at maritime ports, airports and border crossings. Positive detections of insects, plant pathogens, noxious weeds and other plant pests are recorded in the 'Port Information Network' database (PIN) that has been maintained by APHIS since 1984. However, because detection priorities vary depending on pests or commodities of current concern and negative interceptions are not recorded, PIN data are not statistically valid for estimating approach rates of nonindigenous species.

In 1997, USDA-APHIS implemented an additional sampling strategy aimed at detecting nonindigenous plant pests called the Agricultural Quarantine Inspection Monitoring (AQIM) protocol (Venette et al. 2002). AQIM monitoring is based on a random, hypergeometric protocol for sampling cargo within containers and provides a statistically valid method for detecting nonindigenous pests infesting greater than 10% of a shipment with 95% confidence (Venette et al. 2002). Given the large volume of imported material arriving at ports and pressure to quickly inspect perishable cargo, AQIM inspectors are able typically able to examine up to 20-25% of randomly selected cargo (Venette et al. 2002). Unlike inspections recorded in the PIN database, however, AQIM protocols specify random sampling of cargo containers and both negative and positive results of inspections are recorded. Because of this, AQIM data can be used to estimate the number of nonindigenous species that may be arriving within cargo containers but remain undetected. In addition, the AQIM data may be used to evaluate the effectiveness of current efforts aimed at quantifying the influx of nonindigenous plant pests through cargo pathways into the United States.

Here we summarize interceptions of insect species from AQIM inspections conducted between 1 October 1997 and 30 September 2001 for refrigerated and nonrefrigerated maritime cargo, air cargo and cargo crossing the US-Mexico border. These data were used to estimate approach rates of nonindigenous insect species through the four different pathways and to evaluate whether current monitoring efforts implemented by USDA-APHIS adequately characterize the number of nonindigenous insect species associated with the four specific pathways. Finally, we estimate how many nonindigenous species that arrived in the US may have become established between 1997 and 2001.

Materials and methods

AQIM sampling

During AQIM inspections, APHIS personnel sample cargo in shipments that arrive *via* maritime vessels (ships), air transport, and in land vehicles (trucks and automobiles) crossing the US–Mexico border. Vehicles crossing the US–Canada border and rail cargo have been included in AQIM monitoring since 1997, but only at approximately 5% of the border crossings from Canada. Consequently, very little information on pest interceptions from Canada exists relative to other pathways, so these data were excluded from our analysis.

Because products transported through different cargo pathways vary significantly in quantity, size and shape, the sampling units used for AQIM monitoring also vary. For air cargo, the sampling unit is the collection of items described by the accompanying airway bill for a given shipment, which can be as large as 20 m^3 . Sampling units for maritime cargo are containers that are typically 38.5 or 77.0 m³. Sample size for cargo transported by land vehicles ranges from small trucks (approximately 3 m^3) to large tractor-trailers (approximately 120 m^3).

Within each cargo pathway, samples are subdivided into categories defined by the commodities transported. For maritime pathways, AQIM inspectors sample refrigerated cargo containers (4.4 °C) and nonrefrigerated cargo containers containing commodities of agricultural interest, including solid wood packing material. Empty cargo containers and containers with nonagricultural commodities that are considered low risk for the introduction of nonindigenous species by APHIS are also inspected. Within the maritime pathways, most insect interceptions were associated with refrigerated and nonrefrigerated agricultural cargo. Nonindigenous insects were not intercepted within the 606 empty maritime containers or the 883 'low risk' cargo containers inspected (Table 1). For cargo transported by air or trucks, APHIS personnel collect samples from all agricultural commodities that may harbor plant pests and from nonagricultural cargo (typically manufactured goods) that may be packed in solid wood packing materials that can harbor plant pests. On nonagricultural cargo in the air cargo pathway, there was a single interception of a katydid identified only to the genus Neoconocephalus (Orthoptera, Tettigoniidae, Table 1). When vehicles cross the US-Mexico border, agricultural and nonagricultural cargo is inspected, along with empty truck boxes and low-risk agricultural cargo. Within the low-risk agricultural cargo crossing the US-Mexico border, only four insect interceptions were encountered, and only one of these interceptions was identified to species as the melonworm (Diaphania hyalinata L., Lepidoptera, Pyralidae) (Table 1). Due to the relatively small number of interceptions within several cargo pathways, we focused our analysis on the four main pathways that contained cargo of agricultural interest, including refrigerated maritime cargo, nonrefrigerated maritime cargo, air cargo, and US–Mexico border cargo. Random selection of containers within each of these categories is based on the total number of containers available on the randomly determined day scheduled for sampling (Venette et al. 2002).

Manifested cargo commodities that arrived in the four pathways originated from a total of 291 different points of origin (Table 1). Occasionally, commodities are 'double-designated' (e.g. peas or snow peas) because of ambiguous manifest records and cargo classifications or errors in data recording by inspectors. The total number of commodity origins recorded in the AQIM database, therefore, represent the upper limit of potential origins within each pathway.

Statistical analysis

For our analysis, only taxonomic units with valid species names or single interceptions of unique genera were included. Given the volume of cargo material and the requirements for quick inspections of perishable cargo, the number of individual insects of a given taxa associated with a single, positive interception is rarely counted. As such, abundance of insect taxa recorded for AQIM inspections are inappropriate for statistical comparisons, but can be compared as presence– absence sampling once abundance data is power transformed using the value zero for the exponent.

Table 1. Number of containers inspected, number of insect interceptions, points of origin and valid species or single genera interceptions reported for cargo arriving in maritime transport, air transport, and land transport across US–Mexico border and between fiscal year 1997 and 2001.

Transport type	Cargo type	Number of con- tainers inspected	Number of insect interceptions	Number of points of origin	Number of insect taxonomic designations	Number of species
Maritime	Empty container	606	0	0	0	0
	Nonagricultural	883	0	0	0	0
	Nonrefrigerated containers	6459	125	35	70	46
	Refrigerated containers	2578	208	22	80	49
Air	Agricultural	4150	142	28	46	19
	Nonagricultural	1266	2	2	2	1
US–Mexico border	Low-risk agriculture	4902	5	1 (Mexico)	4	3
	Empty container	2407	0	0	0	0
	Nonagricultural	1019	0	0	0	0
	Agricultural	5093	77	1 (Mexico)	25	13

To evaluate the effectiveness of AOIM monitoring at characterizing the nonindigenous insect fauna arriving with imported cargo, we estimated species richness using rarefaction procedures. We used rarefaction based curves rather than species accumulation curves to avoid both known biases as well as unknown biases in the specific order of samples chosen that may affect shape of species accumulation curves. Estimates of the number of species arriving through refrigerated and nonrefrigerated maritime cargo, air cargo, and US-Mexico border pathways were obtained using sample-based rarefaction calculated using Estimates software (Colwell and Coddington 1994; Colwell 1997). We used rarefaction methods to determine whether the estimated number of species associated with a given pathway lies near the asymptote of the rarefaction curve, rather than for direct comparisons of species richness among different cargo pathways. This enabled us to avoid problems of interpretation associated with individual and sample-based rarefaction curves (Gotelli and Colwell 2001). Sample-based rarefaction curves yield identical results for a particular dataset regardless of whether presence/ absence data or species abundance data are used in rarefaction analysis.

We used three sets of rarefaction curves to evaluate the 'best-case', 'probable-case' and 'worstcase' scenarios of the number of species arriving within each pathway. Estimates of species richness in the 'best-case' scenario come from samplebased rarefaction of the observed number of interceptions detected through AQIM inspections. This is referred to as the 'best-case' scenario because this estimate of species richness corresponds to the number of species that would arrive if current sampling efforts were sufficient to detect all of the species arriving through each pathway. In this case, the observed rarefaction curves only represent the 'best-case' scenario if they reach the rarefaction asymptote. If these estimates do not reach the rarefaction asymptote, they indicate that sampling is inadequate to characterize the number of species and likely underestimate the number of species arriving in each pathway.

In cases where observed rarefaction curves did not reach an asymptote, the slope of the linear portion of the rarefaction curve was estimated using a linear regression model (Splus 2000; MathSoft Inc). The inverse of the slope of rarefaction curve can be interpreted as the number of inspections required to observe an incremental increase in the number of arriving nonindigenous species, within the range of shipments inspected for a given pathway. Thus pathways with greater arrival rates require fewer samples to observe an incremental increase in the number of nonindigenous species.

The 'probable' and 'worst' case scenarios are calculated using 'Chao 2' estimators of species richness to assess the number of nonindigenous species that would likely be encountered if sampling effort of cargo containers was increased. The nonparametric Chao 2 estimator provides estimates of species richness in presence/absence datasets that have many 'rare' species, such as the AQIM inspection dataset, by upweighting singleton and doubleton collections (Chao 1987; Colwell and Coddington 1994). The effect of the weighting is to accelerate the approach of the rarefaction curve towards an asymptote, which provides an estimate of the number of species that would have been observed given increased sampling effort (Colwell and Coddington 1994). We chose to use the Chao 2 estimator specifically because it is relatively more sensitive to datasets containing many rare species at low sample sizes than other measures such as the Jacknife 2 estimator (Colwell and Coddington 1994; Anderson and Ashe 2000) and because it generates equivalent results to more computational complex estimators such as the incidence-based coverage estimator (ICM) (Chao and Lee 1992; Lee and Chao 1994; Foggo et al. 2000).

The use of Chao 2 estimators is particularly important in estimating the efficiency of AQIM inspections if the observed rarefaction curves do not reach a species accumulation asymptote. For our analysis, the Chao 2 estimates of species richness can be considered as the number of species that are detected by AQIM inspections as well those species which escaped detection within a given pathway. This represents a 'probable-case' estimate of species arriving in each pathway. Likewise, the Chao 2 estimates of species richness +1 standard deviation may be considered the upper limit of the total number of species (both detected and undetected by AQIM inspections) or the 'worst-case' scenario within a given pathway. The range of species richness expressed by observed species richness and Chao 2 estimates and its associated standard deviation may be interpreted as the 'best-case', 'probable', and 'worst-case' scenarios for the arrival of species within individual pathways.

The efficiency of AQIM inspections within each cargo pathway was evaluated as the range between the number of observed species divided by the Chao 2 estimate of species richness and the number of observed species divided by the Chao 2 estimate +1 standard deviation. Inspection efficiency measured in this way is meaningful only if Chao 2 estimates of species richness have reached the asymptote of the rarefaction curve within a given pathway.

Results

Between fiscal years 1997 and 2001 APHIS personnel used AQIM protocols to sample a total of 29,139 cargo shipments, including 5416 arriving by air, 13,421 by land-vehicles, and 10,572 by maritime vessels (Table 1). Of the 529 positive insect interceptions, the level of taxonomic identification of these interceptions varied among pathways. There were 189 insect taxonomic designations reported for all cargo inspections. This included 69 interceptions that were identified to species, 86 identified to genera, and 34 identified only to family accounting for 23, 41 and 35% of the interceptions, respectively (Table 1).

Observed species richness increased linearly with increased inspections for all cargo pathways but never reached the species accumulation asymptote (Figure 1). Arrival rates of nonindigenous species were greatest in refrigerated containers carrying agricultural commodities in maritime cargo. Within this pathway, a new species was observed on average every 50.5 inspections (Table 2). The detection frequency for nonindigenous species entering the US *via* nonrefrigerated maritime cargo, agricultural air cargo, and agricultural cargo across the US–Mexico border was one out of every 129.9, 204.1, and 370.4 inspections, respectively (Table 2).

Observed arrival rate of new species was related to the variety of commodities with positive insect interceptions. Within maritime refrigerated cargo, insects were intercepted on 26 different agricultural commodities (Figure 2). Refrigerated maritime containers carrying peas were associated with the most insect interceptions (21%) (Table 2), but insect interceptions were more evenly distributed among commodities than in other pathways (Figure 2). Within maritime nonrefrigerated cargo, insects were intercepted on 20 commodities (Figure 2). Marble and ceramic tiles accounted for roughly half (50.7%) of the interceptions within this pathway insect (Table 2). Most insect interceptions in the eight commodities shipped as air cargo were associated with cut flowers (68.9%) (Table 2). In US-Mexico border cargo, insects were intercepted on only five commodities and 75% of these interceptions were associated with ornamental palms (Chameadorea spp. Figure 2, Table 2).

Projected estimates of the total number of nonindigenous species, which includes undetected species, were highly variable among pathways (Figure 3). Estimates of species richness in maritime refrigerated containers ranged from 49 (observed) to 1776 (Chao 2 + 1 SD) species and increased with increasing sample size (Figure 3). Likewise, estimates of species richness in agricultural air cargo ranged from 19 (observed) to 221 (Chao 2 + 1 SD) species and increased with increasing sample size. Because the Chao 2 estimates of species richness continued to increase with sample size, AQIM sampling efficiency could not be evaluated within these pathways.

Projected estimates of species richness in nonrefrigerated maritime containers and US-Mexico border cargo were less variable than refrigerated maritime and air cargo and may have begun to approach their respective species accumulation asymptotes (Figure 3). This suggests that a lower limit to the number of species being intercepted can be estimated given the data collected through AQIM within these pathways. Projected estimates of species richness arriving in nonrefrigerated maritime cargo containers ranged from 46 (observed) to 237 (Chao 2 + 1 SD) species with a 'probable' estimate of 163 species (Chao 2) (Figure 3b). Inspection of projected rarefaction curves shows that following 4500 inspections, Chao 2 estimates of species richness increased by 27 (or 16% of the total estimate) in the remaining 1959 inspections. Projected estimates of species richness in US-Mexico border cargo ranged from 13 (observed) to 42 (Chao 2 + 1 SD) species with a 'probable' estimate of 27 (Chao 2) species (Figure 3d). Following 3200 inspections, Chao 2 estimates of species richness varied from 27 to 35



Number of Inspections

Figure 1. Observed rarefaction curves for nonindigenous insect species ('best-case' scenario, solid line) ± 1 SD (dotted lines) for (a) refrigerated and (b) nonrefrigerated maritime cargo, (c) air cargo, and (d) border cargo transported across the US–Mexico border.

Table 2. Linear regressions of observed species accumulation functions for agricultural air cargo (n = 4148), agricultural cargo intercepted crossing the US-Mexico border (n = 5091), and nonrefrigerated (n = 6457) and refrigerated containers arriving on maritime vessels (n = 2576).

Pathway	Cargo type	Intercept (±SD)	Slope (±SD)	Number of cargo units giving new species (1/slope)	R ²	Number of commodities within each pathway with interceptions	Dominant commodity
Air	Agricultural	1.636 (0.0195)	0.0044 (0.0000)	227.27	0.9857	8	Cutflowers 68.9%
US–Mexico border	Agricultural	0.407 (0.0074)	0.0026 (0.0000)	384.62	0.9952	5	<i>Chameadorea</i> sp.75.0%
Maritime	Nonrefrigerated containers	2.528 (0.0315)	0.0071 (0.0000)	140.85	0.9909	20	Tile 50.7%
	Refrigerated containers	1.944 (0.0183)	0.0186 (0.0000)	53.76	0.9989	26	Peas 21.1%

species with a mean of 31 species in the remaining 1593 inspections. These estimates suggest that AQIM sampling detects 19.4–28.2% of the species arriving within nonrefrigerated maritime cargo and 30.9-54.1% of the species arriving in cargo across the US–Mexico border.



Figure 2. Relative abundance of insect interceptions ranked by commodities transported through (a) refrigerated and (b) nonrefrigerated maritime cargo, (c) air cargo, and (d) border cargo transported across the US-Mexico border.

Discussion

Both the observed and projected arrival rates suggest that significant numbers of nonindigenous insect species remain undetected, particularly in refrigerated maritime cargo and air cargo. Because estimated species richness increased nearly linearly with inspection effort and did not asymptote at a specific value and because AQIM monitoring protocols were designed only to detect infestations of greater than 10% of a given shipment, it is likely that our estimate of the upper range of arrival rates via these pathways is conservative. Despite the seemingly impossible task of detecting all nonindigenous species transported in these pathways, we are encouraged by the fact that the estimated species richness on nonrefrigerated maritime cargo and southern border traffic increased slowly with increasing sample size. This indicates that a detectable upper limit for species arriving through these pathways can be identified and the effectiveness of AQIM monitoring can be evaluated. With the current inspection effort, AQIM monitoring captures approximately 30.9–54.1% of the species arriving in cargo crossing the US-Mexico border and 19.4-28.2% of the actual species arriving via the nonrefrigerated maritime

cargo pathway. Differences in monitoring efficiency between nonrefrigerated maritime cargo and US–Mexico border cargo may be due to the common use of solid wood packing material in nonrefrigerated maritime containers, where nonindigenous species can be difficult to detect (Haack 2001).

We initially hypothesized that diversity of nonindigenous insect species associated with specific pathways might be related to the variety of commodities that were imported or the number of countries where commodities originated. Relative rates of arrival and estimations of nonindigenous species richness, however, were not consistent with the number of commodities or points of origin described on shipping manifests among the four pathways. For example, while arrival rate and estimated number of species was greatest in the maritime refrigerated cargo, this pathway transported the fewest types of commodities $(\sim 350 \text{ commodities})$ and these containers originated from relatively few points of origins (72 different countries). Nonrefrigerated maritime cargo pathway had the second highest rate of arrival and estimated nonindigenous species richness, but included the largest variety of commodities (~2700 commodities) from the second greatest number of origins (151 different countries).



Figure 3. Projected estimate of total number of species arriving (Chao 2 estimator, 'probable case' scenario, solid line), and upper limit of projected estimates of total number of species arriving (Chao 2 estimator ± 1 SD, 'worst case' scenario, dashed line) for (a) refrigerated and (b) nonrefrigerated maritime cargo, (c) air cargo, and (d) border cargo transported across the US–Mexico border.

Likewise, within the air cargo pathway, over 1500 different commodities were imported from 153 different countries, yet this pathway ranked third in arrival rates and estimated nonindigenous species richness. Finally, the pathway with the smallest arrival rate and estimated nonindigenous species richness was the US-Mexico border where over 700 different commodities were imported. In all cases, Mexico was recorded as the only point of origin of these commodities. Relationships between the number of origins or commodities and arrival rates of nonindigenous insect species, therefore, remain ambiguous. This may be partly attributable to inaccuracies in reporting or recording the contents of cargo containers, which will limit the use of manifest records for characterizing factors associated with high arrival rates of nonindigenous species.

Although unrelated to the total commodities manifested within a pathway, increasing numbers of positive insect interceptions were associated with a larger 'suite' of commodities. In maritime refrigerated cargo, positive insect interceptions were more evenly distributed among a greater number of commodities than in other pathways. This suggests that the variety of commodities transported through this pathway may affect the risk of pest introduction or that the pathway itself is relatively more likely to facilitate survival and arrival of nonindigenous species. In contrast, within the other three pathways examined, a single commodity was associated with over 50% of the total interceptions. For example, insect interceptions in the nonrefrigerated maritime pathway were most commonly associated with tile products, primarily imported from Italy and other Mediterranean countries (J. Cavey et al. unpublished data). Within pathways where the majority of positive insect interceptions were confined to a single commodity, monitoring and exclusion effort can be concentrated on specific commodities such as tiles in nonrefrigerated maritime containers, cutflowers in air cargo, and ornamental palms transported across the US–Mexico border.

Methods of packing and shipping may play an important role in determining arrival and survival rates of nonindigenous species. For example, 19% of insects intercepted on maritime cargo entering New Zealand were alive upon reaching port destinations (Stanaway et al. 2001), while previous estimates of insect survivorship in air cargo entering Hawaii were much lower (<1%) (Rainwater 1963). Presumably insects introduced in refrigerated containers may survive at relatively high rates, increasing the risk associated with this pathway, because containers are kept at constant, nonlethal temperatures throughout transport.

Estimates of establishment rates for nonindigenous species that have arrived in new habitats have ranged from 2% for accidental introductions (di Castri 1989) to 65% for some biological control introductions (Crawley 1989). If a conservative estimate of 2% establishment is used, then as many as 34 species introduced via refrigerated maritime cargo may have become established in the US between 1997 and 2001. Extending this calculation, 4, 3, and <1 nonindigenous species may have become established in the US, via air cargo, nonrefrigerated maritime cargo, and cargo from Mexico, respectively. Accuracy of these predictions will likely be tested in the next several years once sufficient time has elapsed for these established populations to be detected (National Research Council 2001).

Acknowledgements

We would like to thank USDA-APHIS for access to AQIM data and the Pathways group at the National Center for Ecological Analysis and Synthesis (NCEAS) for constructive and insightful discussions. We would also like to thank D. Marshall, R. Haack, J. Spence, D. Shorthouse and B. Dankert for their thoughtful comments on earlier versions of this manuscript. This work was conducted as part of the Invasion Pathways Working Group supported by the National Center for Ecological Analysis and Synthesis, a center funded by NSF (Grant #DEB-0072909), the University of California, and the Santa Barbara campus.

References

- Anderson RS and Ashe JS (2000) Leaf litter inhabiting beetles as surrogates for establishing priorities for conservation of selected tropical montane cloud forests in Honduras, Central America (Coleoptera; Staphylinidae, Curculionidae). Biodiversity and Conservation 9: 617–653
- Byers JE, Reichard S, Randall JM, Parker IM, Smith CS, Lonsdale WM, Atkinson IAE, Seastedt TR, Williamson M, Chornesky E and Hayes D (2002) Directing research to reduce the impacts of nonindigenous species. Conservation Biology 16: 630–640
- Calcott A-MA and Collins HL (1996) Invasion and range expansion of imported fire ants (Hymenoptera: Formicidae) in North America from 1918–1995. Florida Entomologist 79: 240–251
- Carlton JT and Geller JB (1993) Ecological roulette; the global transport of nonindigenous marine organisms. Science 261: 78–82
- Chao A (1987) Estimating the population size for capturerecapture data with unequal catchability. Biometrics 43: 783-791
- Chao A and Lee SM (1992) Estimating the number of classes *via* sample coverage. Journal of the American Statistical Association 87: 210–217
- Colwell RK (1997) Estimates: Statistical Estimation of Species Richness and Shared Species from Samples. Version 5. User's Guide and Application published at: http://viceroy. eeb.uconn.edu/estimates
- Colwell RK and Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London B Biological Sciences 345: 101–118
- Crawley MJ (1989) The population biology of invaders. Philosophical Transactions of the Royal Society of London B Biological Sciences 314: 321–359
- di Castri F (1989) History of biological invasions with special emphasis on the old world. In: Drake JA (ed) Biological Invasions: a Global Perspective, pp 1–30. Wiley and Sons
- Foggo A, Rundle SD and Bilton DT (2003) The net result: evaluating species richness extrapolation techniques for littoral pond invertebrates. Freshwater Biology 48: 1756–1764
- Galil BS and Hulsmann N (1997) Protist transport *via* ballast water – Biological classification of ballast tanks by food web interactions. European Journal of Protistology 33: 244–253
- Gollasch S (2002) The importance of ship hull fouling as a vector of species introductions into the North Sea. Biofouling 18: 105–121
- Gotelli NJ and Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379–391

- Hallegraeff GM and Bolch CJ (1992) Transport of diatom and dinoflagellate resting spores in ships ballast water: implications for plankton biogeography and aquaculture. Journal of Plankton Research 14: 1067–1084
- Hulsmann N and Galil BS (2001) The effects of freshwater flushing on marine heterotrophic protists – implications for ballast water management. Marine Pollution Bulletin 42: 1082–1086
- Lee SM and Chao A (1994) Estimating population size via sample coverage for closed capture–recapture models. Biometrics 50: 88–97
- Leppakoski E, Gollasch S, Gruszka P, Ojaveer H, Olenin S and Panov V (2002) The Baltic – a sea of invaders. Canadian Journal of Fisheries and Aquatic Sciences 59: 1175–1188
- Locke A, Reid DM, Vanleeuwen HC, Sprules WG and Carlton JT (1993) Ballast water exchange as a means of controlling dispersal of fresh-water organisms by ships. Canadian Journal of Fisheries and Aquatic Sciences 50: 2086–2093
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M and Bazzaz FA (2000) Biotic invasions: Causes, epidemiology, global consequences and control. Ecological Applications 10: 689–710
- National Research Council (2001) Committee on the Scientific Basis for Predicting the Invasive Potential of Nonindigenous Plants and Plant Persts into the United States. National Academy Press, pp 1–194
- Niemelä P and Mattson WJ (1996) Invasion of North American forests by European phytophagous insects. Bioscience 46: 741–753
- Nowak DJ, Pasek JE, Sequeira RA, Crane DE and Mastro VC (2001) Potential effect of *Anoplophora glabripennis*

(Coleoptera: Cerambycidae) on urban trees in the United States. Journal of Economie Entomology 94: 116–122

- Pierce RW, Carlton JT, Carlton DA and Geller JB (1997) Ballast water as a vector for tintinnid transport. Marine Ecology-Progress Series 149: 295–297
- Pimentel D, Lach L, Zuniga R and Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. Bioscience 50: 53–65
- Rainwater HI (1963) Agricultural insect pest hitchikers on aircraft. Proceedings of the Hawaiian Entomological Society 28: 303–309
- Sailer RI (1978) Our immigrant insect fauna. Bulletin of the Entomological Society of America 24: 3–11
- Shea K and Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17: 170–176
- Stanaway MA, Zalucki MP, Gillespie PS, Rodriguez CM and Maynard GV (2001) Pest risk assessment of insects in sea cargo containers. Australian Journal of Entomology 40: 180–192
- US Congress (1993) Harmful nonindigenous species in the United States. OTA-F-565. Office of Technology, pp 1–397
- Venette RC, Moon RD and Hutchison WD (2002) Strategies and statistics of sampling for rare individuals. Annual Review of Entomology 47: 143–174
- Vitousek PM, Dantonio CM, Loope LL, Rejmanek M and Westbrooks R (1997) Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21: 1–16
- Vitousek PM, Dantonio CM, Loope LL and Westbrooks R (1996) Biological invasions as global environmental change. American Scientist 84: 468–478
- Williamson MH (1996) Biological Invasions. Chapman & Hall, pp 1–224