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Historical data reveal power-law dispersal patterns of invasive aquatic species

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Abstract

Understanding how invasive species spread is of particular concern in the current era of globalisation and rapid environmental change. The occurrence of super-diffusive movements within the context of Lévy flights, has been discussed with respect to particle physics, human movements, microzooplankton, disease spread in global epidemiology and animal foraging behaviour. Super-diffusive movements provide a theoretical explanation for the rapid spread of organisms and disease (Viswanthan, 2010), but their applicability to empirical data on the historic spread of organisms has rarely been tested. This study focuses on the role of long-distance dispersal in the invasion dynamics of aquatic invasive species across three contrasting areas and spatial scales: open ocean (North-East Atlantic), enclosed sea (Mediterranean) and an island environment (Ireland). Study species included five freshwater plant species, *Azolla filiculoides, Elodea canadensis, Lagarosiphon major, Elodea nuttallii and Lemna minuta*; and ten species of marine algae, *Asparagopsis armata, Antithamnionella elegans, Antithamnionella ternifolia, Codium fragile, Colpomenia peregrina, Caulerpa taxifolia, Dasysiphonia sp., Sargassum muticum, Undaria pinnatifida and Womersleyella setacea*. A simulation model is constructed to show the validity of using historical data to reconstruct dispersal kernels. Lévy movement patterns similar to those previously observed in humans and wild animals are evident in the re-constructed dispersal pattern of invasive aquatic species. Such patterns may be widespread among invasive species and could be exacerbated by further development of trade networks, human travel and environmental change. These findings have implications for our ability to predict and manage future invasions, and improve our understanding of the potential for spread of organisms including infectious diseases, plant pests and genetically modified organisms.

Introduction

Modelling the spread of species is a key issue in ecology and has important implications for many fields of environmental change research including palaeoecology (Clark, 1998), invasion biology (Shigesada *et al.*, 1995; Yamamura *et al.*, 2006), epidemiology (Mundt, *et al.* 2009), climate change modelling (Higgins & Harte, 2006) and restoration of degraded landscapes (Nathan *et al.* 2008). In invasion biology, predicting rates of species spread is essential in formulating guidance for managers (Bullock *et al.*, 2008) and in planning national control strategies.

Historically descriptions of patterns of species' spread have been based on classical ‘reaction diffusion' models, which incorporate parameters of species reproduction and dispersal rates. These models suggest that the spread of a population, in terms of the distance from the point of introduction, increases linearly with time (and therefore the square root of the occupied area also increases linearly due to the relationship between area and radius in a two dimensional plane: see Skellam 1951 for mathematical derivations). Reaction diffusion models assume that dispersal kernels conform to a normal distribution (Williamson *et al.*, 2005). However, empirical data on dispersal are frequently leptokurtic (Kot *et al.*, 1996). Rates of spread are extremely sensitive to the frequency of long-distance dispersal events (Shigesada *et al.*, 1995; Clark, 1998; Kot *et al.*, 1996). Indeed, it has been demonstrated that rates of spread can increase by an order of magnitude even when the frequency of long-distance dispersal is extremely low, for example, 0.1 % of dispersal events (Higgins & Richardson, 1999). Classical reaction diffusion models are therefore likely to substantially underestimate rates of spread where long-distance dispersal occurs. In addition, theoretical models suggest that frequent long distance dispersal events may diminish the role of life history traits and landscape factors in determining the rate of species spread (Marco *et al.*, 2011).

Simulations of the evolution of plant dispersal have shown that dispersal curves with a generalized power law form that predict a non-zero probability of propagules dispersing over very long distances are likely to evolve in natural landscapes (Hovestadt *et al.,* 2001). Empirical studies of plant spread have employed power laws to describe wind dispersal of seeds over relatively small spatial scales (e.g. Marco *et al.,* 2011), but have not addressed larger scale patterns that may result from the power law behaviour of human or animal vectors. Scaling up from local dispersal models to those which are applicable across spatial scales is one of the key difficulties in dispersal ecology and requires alternative approaches to those used on small scales (Bullock & Nathan, 2008).

Organisms which spread more rapidly than predicted by classical diffusion are referred to as having super-diffusive properties. One explanation for super-diffusive spread which has garnered much interest in recent scientific literature is the Lévy flight paradigm (Klafter & Sokolov, 2005; Viswanathan, 2010). Lévy flights are characterised by a power law distribution in the occurrence of long-distance dispersal events, the probability $P(\ell)$ of a given dispersal step length (ℓ) occurring is $\approx \ell^{-\mu}$ and the exponent μ is > 1 and ≤ 3. Such Lévy flights predict super-linear rates of spread and have been shown to apply to population-level movements of humans on land (Brockmann *et al.,* 2006; González *et al.,* 2008), cargo ship movements (Kaluza *et al.,* 2010), and the foraging movements of diverse wild animals (Sims *et al.,* 2008; Bartumeus *et al.,* 2010; Humphries *et al.,* 2010).

Human activities are suggested to be the most important long distance vector for plants and animals (Nathan, 2006), with human transport playing a central role in invasion for many species (Catford *et al.,* 2009). Humans have been implicated as a principal long-distance dispersal vector in the spread of both marine and freshwater invasive species. Marine algae are commonly introduced to new regions by maritime traffic and aquaculture, while fishing gear is also likely to influence spread within regions (Williams & Smith, 2007). Freshwater

plants are most commonly introduced through the horticultural trade and may be inadvertently transported on boats or equipment (Keller *et al.*, 2009). However, natural long-distance transportation of some marine species (most notably, in this study, *Codium fragile, Colpomenia peregrina, Sargassum muticum*) may occur by flotation without human aid, and avichory of seeds or vegetative propagules may also be an alternative long-distance vector for some species (e.g. *Azolla filiculoides* and *Lemna minuta*).

Whilst long-distance dispersal is a crucial component in estimating the spread of species (Kot *et al.*, 1996; Higgins & Richardson, 1999; Cain *et al*., 2000; Clark *et al.*, 2003), it is notoriously difficult to quantify directly (Cain *et al*., 2000; Higgins *et al*., 2003) and remains a major challenge in invasion ecology (Hastings *et al*., 2005). This is mainly due to practical difficulties in quantifying rare dispersal events over large geographic areas using seed trapping and mark-recapture techniques. Genetic techniques, including parentage analysis, assignment methods and genealogical approaches have been applied successfully to dispersal kernel estimation (Cain *et al.*, 2000); however, such studies are very labour intensive and many statistical methods are still in development. In addition, these methods are of limited use in the case of introduced species with high levels of clonality, including many freshwater plants, such as those in this study. Conversely, for many invasive species there is a wealth of historical geographic records data available.

We present a simulation model to examine the validity of using historical data to reconstruct step-length distribution patterns (*i.e.* dispersal kernels). Specifically, we examined whether it was possible to distinguish between alternative step-length distributions patterns; exponential, representing thin-tailed dispersal processes; and the Lévy distribution with a power-law tail (also termed Truncated Pareto) representing fat-tailed dispersal processes.

We test the hypothesis that the Lévy flight step-length patterns are evident in the dispersal patterns of aquatic invasive species across spatial scales, using a historical dataset on freshwater and marine invasions, at three spatial scales: open ocean (North-East Atlantic), enclosed sea (Mediterranean) and an island environment (Ireland). This empirical dataset covers a range of species, 5 freshwater and 10 marine algae, which include a wide range of sizes (from less than < 3 mm (*Lemna minuta*) to > 3 m (*Undaria pinnatifida*) in length), reproductive traits and human uses including horticulture, food and aquaria planting (see Supplementary material, Table 1). Finally, the rates of range expansion of each species were examined to determine the link between fat-tailed (Lévy) step-length patterns and non-linear super-diffusive spread.

Methods

Collation of records

We collated a database of location records for the five most common invasive freshwater plant species in Ireland; namely *Azolla filiculoides, Elodea canadensis, Lagarosiphon major, Elodea nuttallii* and *Lemna minuta* (*n* = 2993) (Table 1, Supplementary material Fig. 1), spanning 171 years from 1836 to 2007. More than 98 % of records were at a precision of 1 km or less, the remaining records were recorded at a precision of 10 km. In addition we used location records of invasive marine algae from an extensive dataset (Mineur *et al*., 2010). Species were chosen for inclusion on the basis of having a sufficient number of records (> 50) (see Clauset *et al.* 2009) and being readily identifiable. Generalist habitat requirements and the widespread availability of suitable habitat across the study region were considered to be essential criteria for species inclusion. We selected ten of the most common invasive marine algae in the Mediterranean and European North Atlantic regions from this dataset for inclusion in this study namely *Asparagopsis armata, Antithamnionella elegans,*

Antithamnionella ternifolia, Codium fragile, Colpomenia peregrina, Caulerpa taxifolia, Dasysiphonia sp., Sargassum muticum, Undaria pinnatifida and *Womersleyella setacea* (*n* = 1571) (Table 1, Supplementary material Figs. 2 and 3), spanning 153 years from 1853 to 2006. Location data were provided in WGS 1984 format to a precision of 4 decimal places. All location records were assumed positive at all dates after first recording.

Dispersal step-length distributions

We measured dispersal step-length distances of freshwater species as the shortest Euclidean distance from each new record to a previous record of the same species. This is likely to provide a conservative estimate of long distance dispersal, as some individuals may have dispersed from more distant populations. Further, we used Euclidean distances rather than distances by water as human movements over land have been previously shown to be a common vector for invasive freshwater species (Buchan & Padilla, 1999). In our study we also found that many new records of our freshwater species were not connected by waterways, and therefore it was feasible and logical to assume that transportation had occurred across land. In this sense, Ireland is unusual in European terms in that major catchments are not usually connected by canals. We included all records of each species, except *E. canadensis*, which had spread to more than 90 % of the region within 151 years, hence only the first 150 years of records were used representing the initial colonisation period. We calculated distances between marine species records as the shortest distance by sea (*i.e.* without crossing land). For eight of the eleven marine datasets, we calculated distances between records using the Pathmatrix 1.1 (Ray, 2005) extension for ArcGIS 3.2. These records were converted from WGS 1984 to the projected coordinate system ETRS 32 UTM (zone 32N) prior to distance calculations. We calculated distances between records for the remaining three marine species (*A. armata*, *C. fragile* and *S. muticum*) in R 12.2.2 using

the ‘gdistance’ package, due to computational constraints on large datasets in the Pathmatrix package. Distances for these species were calculated using a 0.02 degree cell raster grid. Inaccuracies in distance measurements arising from WGS 1984 were corrected for using the geocorrection function within the ‘gdistance’ package.

Dispersal step-length analysis

We used Maximum Likelihood Estimation (MLE) to fit power law, truncated power law (truncated Pareto) and exponential distributions to the dispersal step-length distribution of each species. The methodology employed here is described in detail in Humphries *et al.* (2010). Briefly, we used an iterative method in each case to derive the best fitting value for the remaining parameters (*i.e.* $x_{\min}$ for power law and exponential, and $x_{\min}$ and $x_{\max}$ for truncated Pareto). This resulted in reduced datasets in each case which included only the data that the distribution was deemed to fit. To enable robust model selection, MLE was used to fit each alternative, competing distribution to each reduced dataset (e.g. exponential and Pareto in the case of best-fitted truncated Pareto dataset) from which log-likelihoods and Akaike’s Information Criteria weights (*w*AIC) could then be calculated. The analysis of each data set therefore resulted in four pairs of *w*AIC: two pairs for the best fitting truncated power law vs. exponential (and vice versa) and two pairs for the best fitting exponential vs. power law (non-truncated) and vice versa.

We initially categorised datasets as Lévy or exponential based on the *w*AIC of the best fitting exponential vs. truncated Pareto and best fitting truncated Pareto vs. exponential. Where one model was the best fit in both tests, that model was considered best for the dataset. In some cases, the exponent of the truncated Pareto distribution was < 1 (*i.e.* outside the Lévy range), so it was not possible to calculate the log-likelihood or *w*AIC. In other cases there was a conflict between the *w*AIC results of the two tests and the best fitting exponential

vs. power law (non-truncated) was compared with the best fitting power law (non-truncated) vs. exponential results. If the exponential model performed better than the power law in both tests, the dataset was deemed to be exponential. All other datasets were considered unclassified, as they could not be assigned to either Lévy or exponential step-length distributions with confidence.

An underlying assumption of random walk analyses is that there is no strong relationship between the frequency distribution of step-length distances and time (e.g. that the pattern is not arising as the result of a few long-distance transport events at the end of a time-series characterised by short step-lengths). To ensure that this was not the case here, we visually assessed the pattern of step-lengths against time (see Supplementary, Fig. 4), and conducted a Spearman's rank correlation test on step-length distances (standardised by species mean and standard deviation) against time. The correlation between step-length distance and time was very low (rho = - 0.073), indicating no strong relationship between step-length and time in this dataset.

Simulation model

To our knowledge, the Lévy flight framework has not been previously applied to empirical data on the dispersal of plants, or indeed to movement networks inferred from maps detailing historical invasion patterns. To explore the validity of the method we developed a simulation environment to generate records of historic invasion. Specifically, our simulation tested whether assigning dispersal distances based on the closest previous invasion record reproduced the original dispersal kernel with sufficient accuracy to distinguish between Lévy flight (fat-tailed) and exponential (thin-tailed) dispersal patterns. Simulations were applied in R 12.2.2.

Our models simulated the spread of a hypothetical invasive species based on alternative movement patterns of vectors (exponential and power law). The model was applied within the terrestrial boundary of Ireland (as used in the empirical study of freshwater invasions). The mean values of fitted power-law and exponential distributions in the empirical freshwater species datasets were used as prior parameters for candidate distributions. Initially, the simulation generated a random point of introduction, after which, the spread of propagules was simulated from that location. The number of new propagules at each point was drawn from a Poisson distribution. The Poisson distribution had a mean of 1.5 new records per source point, which was the mean number of the new records occurring in the first ten years after introduction in the freshwater study species. This was repeated for five 'generations' (sufficient to recreate the number of records typical within historic records), with propagules 'reproducing' from every novel 'invasion point' created in the previous 'generation'. The direction of travel followed by each propagule varied randomly. The dispersal distance travelled by each new propagule was drawn from two alternative distributions depending on the process being simulated, namely an exponential distribution (rate = 0.07) representing a Brownian-type diffusion process, or a power-law distribution ($x_{\min}$ = 0.49, exponent = 1.26) representing the Lévy model. Each simulation model was run 100 times. The mean number of resulting points per model was 163 (s.d. = 124).

The resulting simulated invasion data were treated and analysed in exactly the same manner as the empirical freshwater datasets (i.e. dispersal distances were estimated based on the shortest Euclidean distance to a previous point, and dispersal step-lengths were analysed in the same way). In addition, we compared the mean exponents of resulting best fitting distributions with those used in the construction of the simulation to assess whether these could be accurately estimated from the resulting simulated distribution map.

Rates of spread

We calculated the 'invaded area' of each empirical species as the convex hull containing all records of the species at each time point. Convex hulls were calculated using the Geospatial Modelling Environment version 0.5.3 Beta (Hawthorne, 2011) and ArcGIS 10. Convex hulls were clipped to the available range (*i.e.* land mass of Ireland for freshwater species, sea for marine species) using ArcGIS. Spread rates were defined as the increase in the square root of the area within the 'invaded area' over time.

We then fitted linear, 2 parameter exponential and 3 parameter sigmoidal functions to spread rates (square root of 'invaded area' as a function of time since introduction) by MLE. We compared the fits of these three functions using Akaike Information Criteria corrected for small sample sizes (AICc) and corresponding AICc. Linear spread rates represented expected spread under classical reaction diffusion. Initial super-linear rates characteristic of anomalous diffusion were represented by an exponential curve (*i.e.* continuously accelerating spread) and a sigmoid curve (*i.e.* initial accelerating spread followed by a decline in spread rate). This represents the common scenario in natural systems where the observed expansion rate slows as the maximum available range is approached (Mack *et al.*, 2000). Equation fitting and model comparison were conducted in R 12.2.2 (R Development Core Team, 2011) and plotted with SigmaPlot 10 (Systat, 2010).

Results

Simulation analysis

The rate of false positives was 1 % (*i.e.* datasets created from an exponential dispersal distribution that were incorrectly assigned to the Lévy model or vice versa). The rate of true positives was 83 % for Lévy distributions and 82 % for exponential distributions. In the

remaining 16.5 % of cases, results were ambiguous and it was not possible to assign them to either distribution (Supplementary material Table 2). In the empirical data, these were treated as unclassified, as it was unclear whether species had Lévy or exponential dispersal kernels. Additionally, the fitted truncated Pareto (power law) distributions provided a good approximation of the $x_{\min}$ and exponents used to simulate dispersal patterns. In Lévy (truncated Pareto) based simulations the estimated mean exponent of 1.27 (s.d. = 0.43) (generated from 1.26) and the estimated mean $x_{\min}$ of 0.431 (sd = 0.13) (generated from 0.49) recovered the modelled dispersal pattern reasonably well. In exponential based simulations, the estimated mean rate was 0.24 (s.d. 0.07) (generated from 0.07), suggesting that the method of assigning dispersal distances may under-estimate the amount of long-distance dispersal occurring when the real dispersal step-length distribution is exponential. Despite this, the low rate of false positives indicates that the method is useful for distinguishing between historical distribution patterns arising from Lévy (fat-tailed) and exponential (thin-tailed) dispersal step-length distributions.

Dispersal step-length analysis

Three of the five freshwater species were fitted best by the truncated power law and showed exponents within the Lévy range (mean exponent, 1.38 ± 0.15 s.d.). One species, *Lemna minuta*, was fitted best by an exponential, while *Lagarosiphon major* could not be reliably fit best by either model (Table 2, Fig. 2). In eight of the eleven invasions of marine algae, dispersal distributions were fitted best by the truncated power law with exponents within the Lévy range (mean, 1.20 ± 0.16 s.d.). Three species (*Antithamnionella ternifolia, Dasysiphonia sp.* and *Undaria pinnatifida*) were not reliably fit best by either model (Table 2, Fig. 2). Maximum step lengths for individual species were between 141 km and 275 km in

freshwater species, and 614 km and 2012 km in marine species, suggesting that population establishment after long-distance dispersal events occurs for all study species across habitats (Table 2).

Rates of spread

Sigmoid curves fit best to the spread rates of the freshwater invasive species - *A. filiculoides* and *E. nuttallii*, and an exponential fit best for *E. Canadensis*, consistent with the finding of Lévy dispersal distributions for these species. *L. major* and *L. minuta* were fitted best by linear spread rates consistent with classical reaction diffusion, although the sigmoidal model had some support for *L. minuta*. In the marine algae, 9 of the 11 spread rates were non-linear (sigmoidal) (Table 3, Fig. 3). Overall, the analysis showed that the vast majority of species had a Lévy distribution of step lengths and exhibited non-linear, initially accelerating spread rates. The spread of *Dasysiphonia sp.* was linear and did not show a Lévy pattern (Fig. 2m). Interestingly, *A. armata* in the Mediterranean was best fitted by a linear spread model, despite its Lévy step-length pattern (Fig 2g, Fig. 3g): however the spread of this species was also well described by a sigmoidal curve (Table 3, Fig. 3g).

Discussion

In this study, we demonstrate through simulation that dispersal step-length distributions (dispersal kernels) of invasive species can be reconstructed from historical distribution data, and that the accuracy of this method is sufficient to differentiate between fat-tailed Lévy step-length dispersal distributions and thin-tailed exponential dispersal distributions. In the great majority of simulation runs, the dispersal distribution used in the model input could be inferred from the spatial pattern of location records outputted by the simulation. The Lévy framework, and especially the use to step-length analysis, is an increasingly common tool used to examine ecological and behaviour processes. Here, it is shown that it can be extended to explore the processes of range expansion and colonisation over both protracted time periods and large spatial scales to extract generalised patterns of invasion biology.

Lévy dispersal patterns were detected in the majority of study species, despite differences in size, reproductive traits and human uses of species. This suggests that Lévy dispersal patterns may be common amongst aquatic plants and algae.

In the case of freshwater plants, Lévy dispersal patterns were coincident with non-linear spread in three species, while *Lagarosiphon major* and *Lemna minuta* showed non-Lévy dispersal and linear spread. *L. minuta* differs from the other freshwater species in that individual plants are very small (< 3mm) and unlikely to be intentionally transported by humans for ornamental or aquaculture purposes. *L. major* belongs to the same family as *Elodea nuttallii* and *Elodea canadensis* and has a very similar morphology and association with human trade. However, *L. major* differs from these species in that it is associated with alkaline conditions: in Ireland 71 % of its recorded distribution is within one lake system (Lough Corrib, Co. Galway). Therefore, the recorded distribution of this species may reflect the availability of this specialized habitat, rather than purely the dispersal dynamics of its vectors.

In eight of the 11 invasions of marine algae, showed Lévy dispersal patterns and seven of these showed concordant sigmoidal non-linear spread. Only one marine species showed a solely linear range expansion (*Dasysiphonia sp.*). This species showed no evidence of a Lévy step-length distribution pattern. While some long-distance jump dispersal events early in the spread of this species have been documented (Mineur *et al.*, 2010), these are not as frequent as would be expected in a Lévy spread pattern. The contrast between the linear spread of *Asparagopsis armata* in the Mediterranean and the sigmoidal spread in the Atlantic is interesting given that it exhibited a Lévy step length distribution in both regions. The cause of this disparity between regions is unclear, but it could result from multiple factors, including those associated with community dynamics, algal life-history traits and environmental conditions (Lyons & Scheibling, 2009). Two further species (*Antithamnionella ternifolia* and *Undaria pinnatifida*) showed no evidence of Lévy patterns, but did have sigmoidal spread. In these cases, there may have been a higher frequency of long distance dispersal than predicted by an exponential model, but not as high as in Lévy models (Figs 2i, 2o).

This study has combined the previously observed high levels of long-distance dispersal in plant populations and invasion ecology with the developing framework of Lévy flight. Whilst the classification of Lévy flights has received significant recent attention in animal foraging ecology (González *et al*., 2008; Sims *et al*., 2007; Humphries *et al*., 2010, Lundy *et al.* 2012), their role in longer term species spread has received relatively little attention.

The super-diffusive patterns of invasive spread by freshwater plants and marine algae may arise as an emergent property of human translocations over land (Gonzalez *et al.* 2008), or by commercial shipping (Kaluza *et al.* 2010) on hulls or in ballast water. Previous studies have suggested a correlation between invasive species human factors such as trade, travel (Catford *et al.*, 2009), population density and gross national product (Keller *et. al*, 2009). Trends in the

trade of particular commodities (*e.g.* aquaculture plants) are also likely to correlate with the rate spread of species (Hulme *et al.* 2009).

Previous studies have reported maximum dispersal distances by non-human transport for plants of 1–20 km (Cain *et al.*, 2000), thus corroborating the likelihood that extreme long-distance transport may be attributable to human transport. However, avichory (seed dispersal by birds) cannot be dismissed as a candidate non-human vector. The seeds of many freshwater aquatic plants remain viable after transport in the intestines of wildfowl and this may account for dispersal over hundreds of kilometres (Brochet *et al.*, 2010). However, more than half of the freshwater species in the current study reproduced by vegetative means only and are probably too large for extensive epizoochory (*E. canadensis, E. nuttallii, L.major*), further supporting the role of humans as the key long-distance vector.

Increases in human trade and transportation during the present period of globalisation may, therefore, increase rates of spread of these species. However, as we found no correlation between step-length distances and year, we suggest that this results from the frequency of introductions, rather than changes in the relative frequency of long-distance transport. However, as this study only investigates European invasion patterns we can not comment on larger global scale patterns between continents.

Furthermore, species traits are likely to influence the extent to which particular organisms can benefit from long-distance dispersal opportunities (Theoharides & Dukes, 2007; van Kluenen *et al.*, 2010). For example, the rare super-diffusive movements of Lévy flight are likely to be of most benefit to organisms that can establish new populations from single introductions, such as, self-fertile and asexually reproducing taxa (*e.g.* clonal plants and many plant pests (e.g. Ash disease *Chalara fraxinea*), and those with short generation times are ideally suited to this condition.

This type of analysis, which relies on detailed geographic records of established populations, is best suited to species with generalist habitat requirements and those species for which suitable habitat is available across the region at the spatial scale of the study, such as generalist invasive species. In the case of specialist species, landscape heterogeneity is likely to confound observed patterns due to its role as a barrier to the establishment of species post-dispersal.

The identification of Lévy patterns does not necessarily imply the existence of a Lévy movement process. It is possible that the observed Lévy patterns arise as the result of a combination of vectors, or vector behaviour, operating at different scales, consistent with the observations of a Lévy distribution of displacements being present at the population-level in human mobility patterns (Brockmann *et al.* 2006; Gonzalez *et al*. 2008, Petrovskii *et al.*, 2011). Similarly, short distance dispersal might be explained by water or wind dispersal, mid-distance by mammals and wind, and long distance by bird or human transport.

Information on the frequency of long-distance dispersal events is essential for the formulation of strategic management plans in invasion biology. This study shows that fat-tailed dispersal patterns with high rates of long-distance dispersal can be inferred from historical data, and occur frequently in aquatic invasive species across large spatial scales. High rates of long-distance dispersal frequently lead to accelerating spread rates (Higgins & Richardson, 1999), increase the difficulty of predicting where invasions will occur next in a landscape (Clark *et al.,* 2003) and may overwhelm the role of life history and landscape heterogeneity in determining rates of spread (Marco *et al.,* 2011). The identification of these patterns in these species emphasizes the importance of focusing management not only on short-distance movements, but also on rarer long-distance vectors which increase uncertainty and cause rates of spread to accelerate, such as trade and transport.

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Tables

Table 1. Dates of introduction, number of records, region and prevalence of study species. MCP denotes minimum convex polygon.

Habitat	Species name	Number of records	Year of introduction	Region	Invasive range MCP (sq. km)
Freshwater	*Azolla filiculoides*	168	1893	Ireland	52,004
	Elodea canadensis	2,348	1836	Ireland	73,952
	Elodea nuttallii	201	1970	Ireland	52,753
	Lagarosiphon major	147	1966	Ireland	66,136
	Lemna minuta	129	1987	Ireland	50,072
Marine	*Asparagopsis armata*	155	1923	Atlantic	623,170
	Asparagopsis armata	118	1923	Mediterranean	1,237,195
	Antithamnionella elegans	67	1882	Mediterranean	2,163,856
	Antithamnionella ternifolia	80	1906	Atlantic	658,072
	Codium fragile	207	1845	Atlantic	1,345,940
	Colpomenia peregrine	104	1905	Atlantic	1,350,104
	Caulerpa taxifolia	86	1984	Mediterranean	628,499
	Dasysiphonia sp.	54	1994	Atlantic	997,160
	Sargassum muticum	544	1972	Atlantic	1,210,447
	Undaria pinnatifida	87	1982	Atlantic	253,584
	Womersleyella setacea	69	1987	Mediterranean	1,191,008

Table 2. Summary of the empirical data and results of MLE fitted to dispersal step lengths, showing best fit parameters and model comparison analysis wAIC. TP and Exp denote truncated Pareto (power law) and exponential models respectively. U is where neither model reliably accounted for the data. TP wAIC is given as NA when TP exponent <1 (outside Lévy range).

Species	N	Min Step Length (km)	Max step length (km)	Best fitting distribution	Best fit exponent	Best fit X-min	Best fit X-max	Exp AIC w	TP AIC w
Azolla filiculoides	135	< 0.1	191	TP	1.54	0.99	191.70	< 0.01	1.00
Elodea canadensis	261	< 0.1	275	TP	1.36	0.49	59.46	< 0.01	1.00
Elodea nuttalli	178	0.1	218	TP	1.23	0.14	218.41	< 0.01	1.00
Lemna minuta	124	0.1	220	E	0.07	0.05	220.62	1.00	NA
Lagarosiphon major	119	0.1	141	U	0.02	0.10	141.61	1.00	NA
Asparagopsis armata (Atl)	118	1.0	1390	TP	1.09	3.83	298.28	< 0.01	1.00
Asparagopsis armata (Med)	155	1.2	1255	TP	1.21	1.24	345.07	< 0.01	1.00
Antithamnionella elegans	67	1.4	2032	TP	1.17	2.41	2032.68	< 0.01	1.00
Antithamnionella ternifolia	80	0.3	1300	U	0.004	79.01	1300.83	0.51	0.49
Codium fragile	207	1.1	865	TP	1.03	1.20	312.56	< 0.01	1.00
Colpomenia peregrina	104	0.1	853	TP	1.01	10.66	470.27	< 0.01	1.00
Caulerpa taxifolia	86	1.0	834	TP	1.34	2.00	258.57	< 0.01	1.00
Dasysiphonia sp.	54	0.2	1015	U	0.003	49.73	1015.23	1.00	NA
Sargassum muticum	544	1.4	612	TP	1.40	1.38	262.70	0.00	1.00
Undaria pinnatifida	87	1.0	805	U	0.01	16.07	805.68	0.55	0.45
Womersleyella setacea	69	0.5	2014	TP	1.35	12.66	1157.64	< 0.01	1.00

Table 3. Model fit of curves describing rates of range expansion and colonisation. n = number of years in which invasion range increased. Grey shading highlights the best fitting function for each species.

Habitat	Species	n	Function	AICc	Δ AIC	% ω_i
Freshwater	*Azolla filiculoides*	24	Linear	251.73	44.08	0
			Exponential	248.91	41.26	0
			Sigmoidal	207.65	0.00	100
	Elodea canadensis	36	Linear	314.86	22.58	0
			Exponential	292.29	0.00	77
			Sigmoidal	294.65	2.36	23
	Elodea nuttallii	16	Linear	153.89	17.87	0
			Exponential	153.14	17.12	0
			Sigmoidal	136.02	0.00	100
	Lagarosiphon major	15	Linear	123.82	0.00	96
			Exponential	142.55	18.74	0
			Sigmoidal	130.20	6.39	4
	Lemna minuta	13	Linear	102.12	0.00	53
			Exponential	105.58	3.42	9
			Sigmoidal	102.79	0.67	37
Marine	*Asparagopsis armata (Atl)*	21	Linear	266.85	22.28	0
			Exponential	274.75	30.17	0
			Sigmoidal	244.58	0.00	100
	Asparagopsis armata (Med)	16	Linear	282.71	0.00	58
			Exponential	296.49	4.92	5
			Sigmoidal	207.68	0.87	37
	Antithamninonella elegans	15	Linear	219.03	23.50	0
			Exponential	206.46	10.93	0
			Sigmoidal	195.53	0.00	100
	Antithamnionella ternifolia	14	Linear	165.55	4.12	11
			Exponential	179.34	17.91	0
			Sigmoidal	161.43	0.00	89
	Codium fragile	28	Linear	342.16	21.69	0
			Exponential	NS	NA	NA
			Sigmoidal	320.47	0.00	100
	Colpomenia peregrina	28	Linear	367.71	55.02	0
			Exponential	384.11	71.42	0
			Sigmoidal	312.69	0.00	100
	Caulerpa taxifolia	8	Linear	109.27	11.36	0
			Exponential	114.72	16.82	0
			Sigmoidal	97.91	0.00	100
	Dasysiphonia sp.	11	Linear	147.57	0.00	92
			Exponential	152.53	4.96	8
			Sigmoidal	NS	NA	0
	Sargassum muticum	24	Linear	293.35	20.59	0
			Exponential	315.34	42.58	0
			Sigmoidal	272.76	0.00	100
	Undaria pinnatifida	13	Linear	150.12	17.69	0
			Exponential	162.66	30.24	0
			Sigmoidal	132.43	0.00	100

Figures

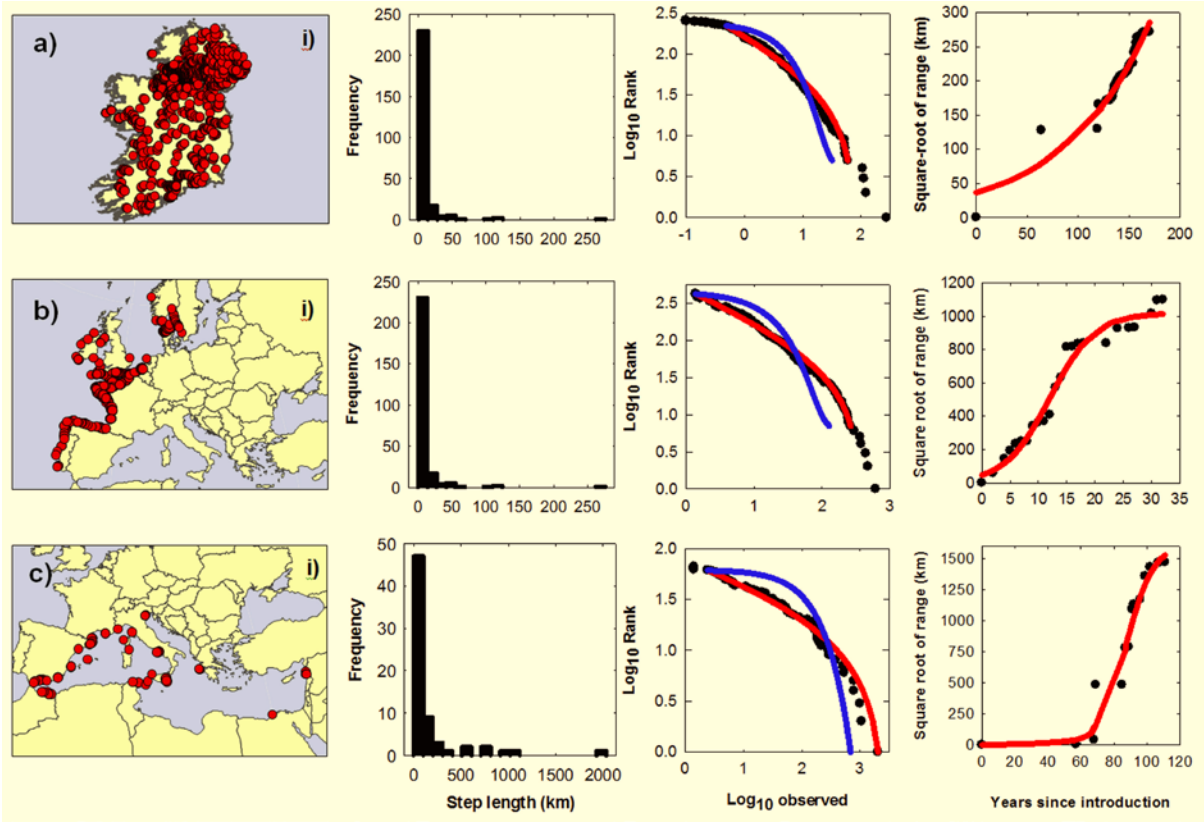

Figure 1 Super-diffusive invasion dynamics of freshwater plants and marine algae. Geographical distributions of **a**, *Elodea canadensis* in Ireland, **b**, *Sargassum muticum* in the north-eastern Atlantic Ocean and **c**, *Antithamnionella elegans* in the Mediterranean Sea, each showing **i)** their geographical distributions, **ii)** a frequency histogram of invasion step lengths, **iii)** competing models showing best fit for a truncated Pareto function (red line) and an exponential function (blue line), and **iv)** non-linear spread based on the increase of the square root of the invaded area over time.

Figure 2 Best fitting models to ranked step-length/frequency plots. Truncated power law (TP) (red line) and exponential (E) (blue line) models to observed data (black circles), or unclassified (U). For details of fitting results see Table 2. Best fit model given in parentheses following species name. Freshwater species: (a) *Azolla filiculoides* (TP); (b) *Elodea canadensis* (TP); (c) *Elodea nuttallii* (TP); (d) *Lagarosiphon major* (U); (e) *Lemna minuta* (E). Marine species: (f) *Asparagopsis armata* (Atl) (TP); (g) *Asparagopsis armata* (med) (TP); (h) *Antithamnionella elegans* (TP); (i) *Antithamnionella ternifolia* (U); (j) *Codium fragile* (TP); (k) *Colpomenia peregrina* (TP); (l) *Caulerpa taxifolia* (TP); (m) *Dasysiphonia sp.* (U); (n) *Sargassum muticum* (TP); (o) *Undaria pinnatifida* (U) and (p) *Womersleyella setacea* (TP).

Figure 3 Spread rates of invasive species. Solid red line indicates best fitting model. Dashed red line indicates second best model where ΔAICc < 2. Freshwater species: (a) *Azolla filiculoides* (sigmoidal); (b) *Elodea canadensis* (exponential); c) *Elodea nuttallii* (sigmoidal); (d) *Lagarosiphon major* (linear); (e) *Lemna minuta* (linear(solid line)/sigmoidal(dashed line)). Marine species: (f) *Asparagopsis armata* (Atl) (sigmoidal); (g) *Asparagopsis armata* (med) (linear(solid line)/sigmoidal (dashed line)); (h) *Antithamnionella elegans* (sigmoidal); (i) *Antithamnionella ternifolia* (sigmoidal); (j) *Codium fragile* (sigmoidal); (k) *Colpomenia peregrina* (sigmoidal); (l) *Caulerpa taxifolia* (sigmoidal); (m) *Dasysiphonia sp.* (linear); (n)

Sargassum muticum (sigmoidal); (o) *Undaria pinnatifida* (sigmoidal); (p) *Womersleyella setacea* (sigmoidal).

Supplementary material

Table 1 Names, size, reproductive traits and human uses of study species

Scientific Name	Common name	Maximum height/length (cm)	Reproduction in invaded European range	Human use in invaded range
Freshwater plants				
Azolla filiculoides Lam.	A water fern	5	Sexual (fern) and vegetative (fragmentation)	Ornamental
Elodea canadensis Michx	Canadensis Pondweed	300	Vegetative (stolons and fragmentation)	Ornamental in horticulture and aquaria
Elodea nuttallii (Planch.) H St. John	Nuttall's Pondweed	300	Vegetative (stolons and fragmentation)	Ornamental in horticulture and aquaria
Lagarosiphon major (Ridl.) Moss	Curly Waterweed	300	Vegetative (stolons and fragmentation)	Ornamental in horticulture and aquaria
Lemna minuta Kunth	A duckweed	0.3	Primarily vegetative (budding), also sexual (dioecious)	
Marine algae				
Asparagopsis armata Harvey	Harpoon Weed	30	Sexual (dioecious), vegetative propagation abundant	
Antithamnionella elegans (Berthold) J.H.Price & D.M.John	A red alga	5	Sexual (dioecious), vegetative propagation abundant	
Antithamnionella ternifolia (J.D.Hooker & Harvey) Lyle	A red alga	5	Sexual (dioecious), vegetative propagation abundant	
Codium fragile subspecies *tomentosoides* (van Goor) P.C.Silva	Green Sea Fingers/ Dead Man's Fingers	50	Parthenogenetic spores	
Caulerpa taxifolia (M. Vahl) C. Agardh	Feather Caulerpa	100	Primarily vegetative	Ornamental in marine aquaria
Colpomenia peregrina Sauvageau	Oyster Thief	15	Sexual (dioecious), vegetative propagation abundant	
Dasysiphonia sp.	A red alga	50	Sexual (dioecious), vegetative propagation abundant	
Sargassum muticum (Yendo) Fensholt	Japanese Wireweed	200	Sexual (Self-fertile monoecious)	
Undaria pinnatifida (Harvey) Suringar	Wakame	300	Sexual (many minute gametophytes)	Food crop
Womersleysella setacea (Hollenberg) R.E. Norris	A red alga	10	Vegetative propagation abundant	

Table 2. Sorting of simulation results based on AICw. E, exponential; TP, truncated power law; P, power law; U, unclassified.

Overall Result	Breakdown of result subset types	Simulation based on exponential dispersal (%)	Simulation based on power law dispersal (%)
Exponential (All)		**82**	**1**
Exponential (subsets)	E better than TP on both tests	2	0
	Conflict between E and TP, and E better than P on both tests	7	1
	Default E, and E better than P on both tests	73	0
Truncated Pareto (All)	TP better than E on both tests	**1**	**83**
Unclassified, U	All other combinations	**17**	**16**

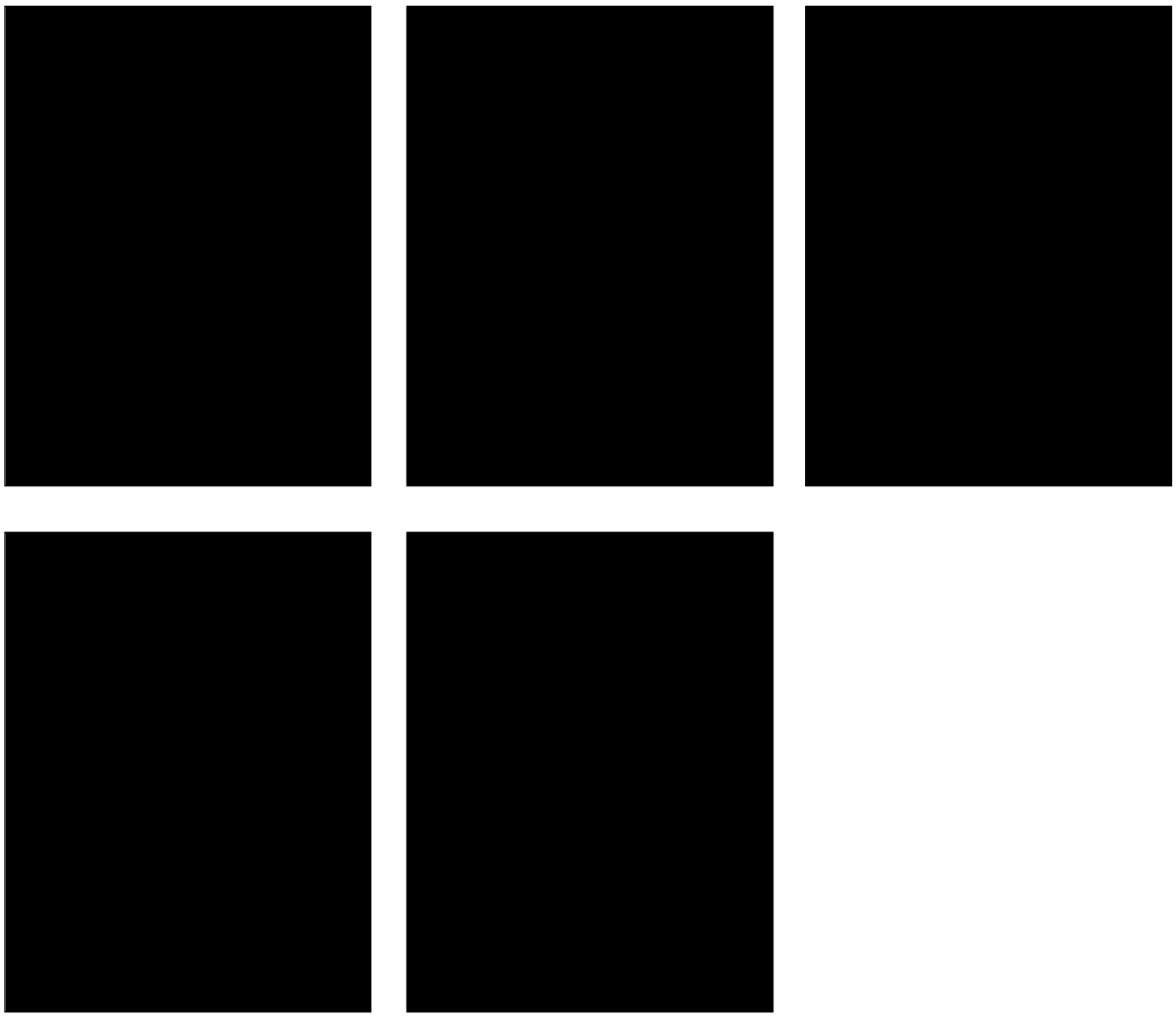

Fig. 1 Locations of freshwater invasive species records in Ireland; a) *Azolla filiculoides*, b) *Elodea canadensis*, c) *Elodea nuttallii*, d) *Lagarosiphon major* and e) *Lemna minuta*.

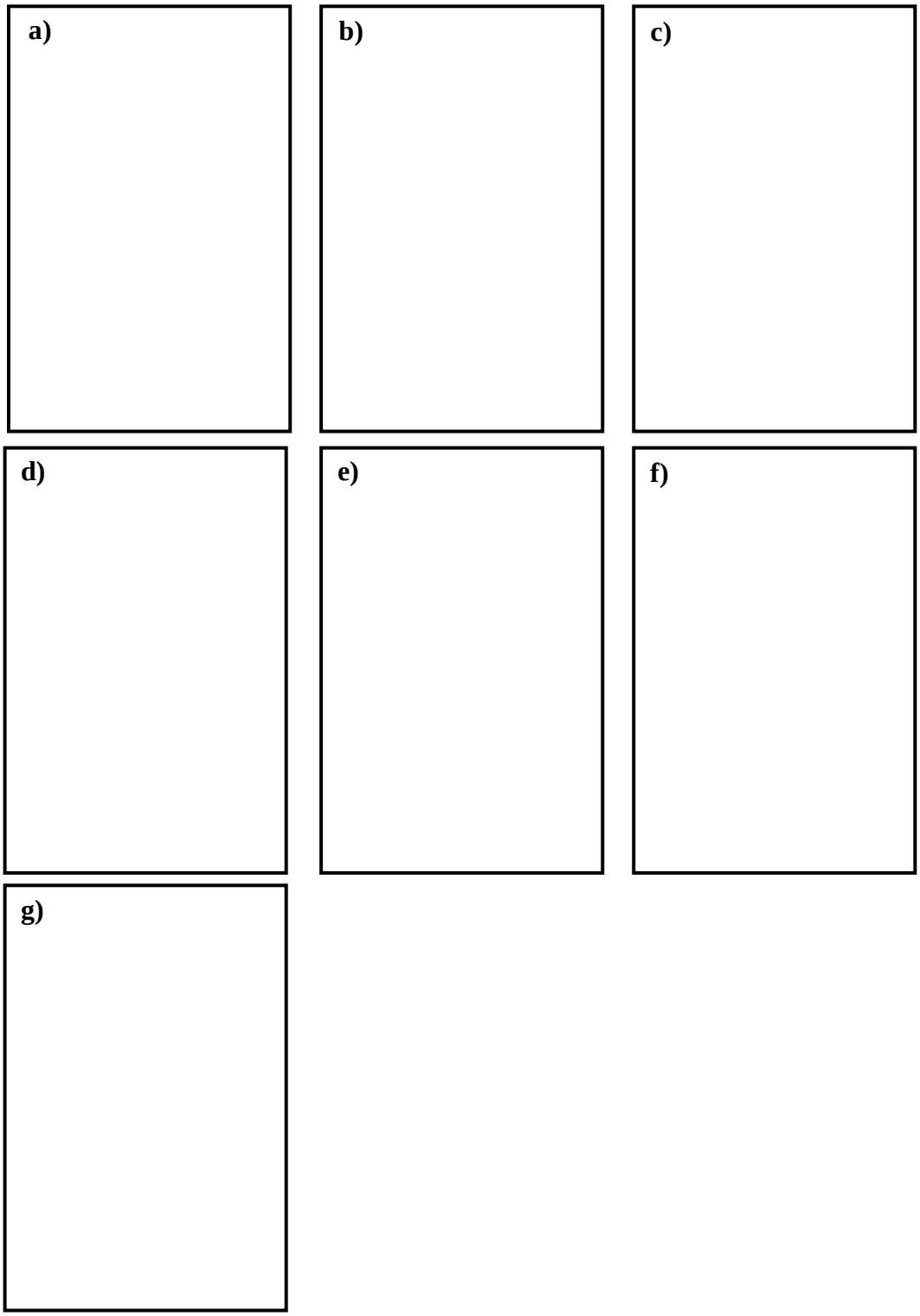

Fig. 2 Distribution of invasive algal species in the Atlantic Ocean. **(**a) *Asparagopsis armata*, (b) *Antithamnionella ternifolia*, (c) *Codium fragile*, (d) *Colpomenia peregrina*, (e) *Dasysiphonia sp.*, (f) *Sargassum muticum* and (g) *Undaria pinnatifida*.

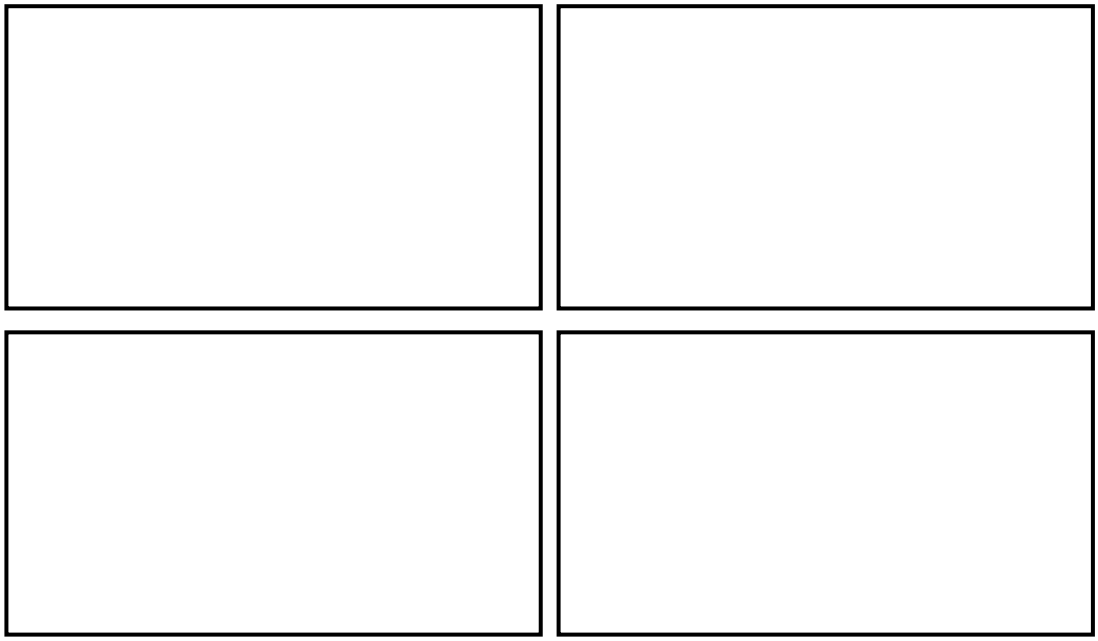

Fig. 3 Distribution of invasive Mediterranean species, a) *Asparagopsis armata*, b) *Antithamnionella elegans,* c) *Caulerpa taxifolia* and d) *Womersleysella setacea.*

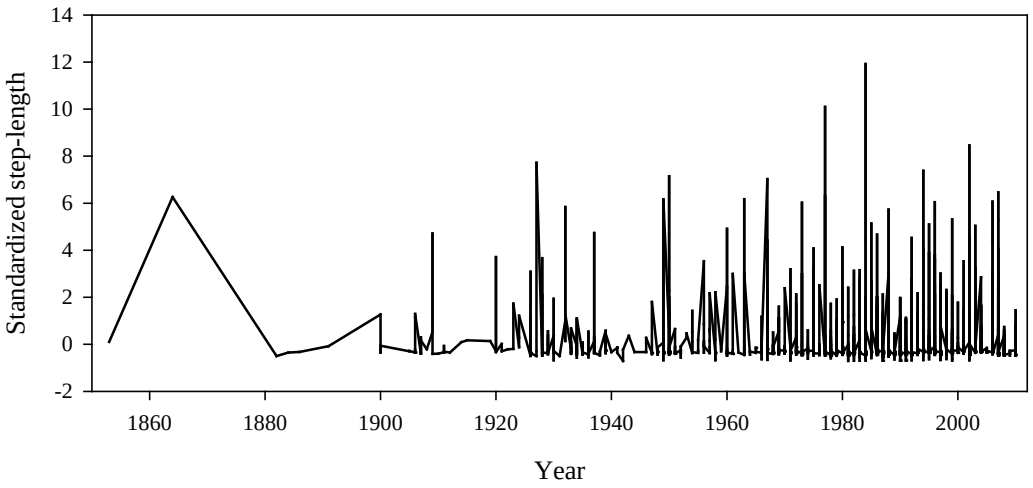

Fig. 4 Distribution of standardised step-length distances across time. Step-lengths of all 16 invasions (11 marine and 5 freshwater) plotted together. Step-lengths standardised to standard deviation in step length within species. Note that, whilst the frenquency of transport increases over time there long distance transport events are evident throughout the time line.

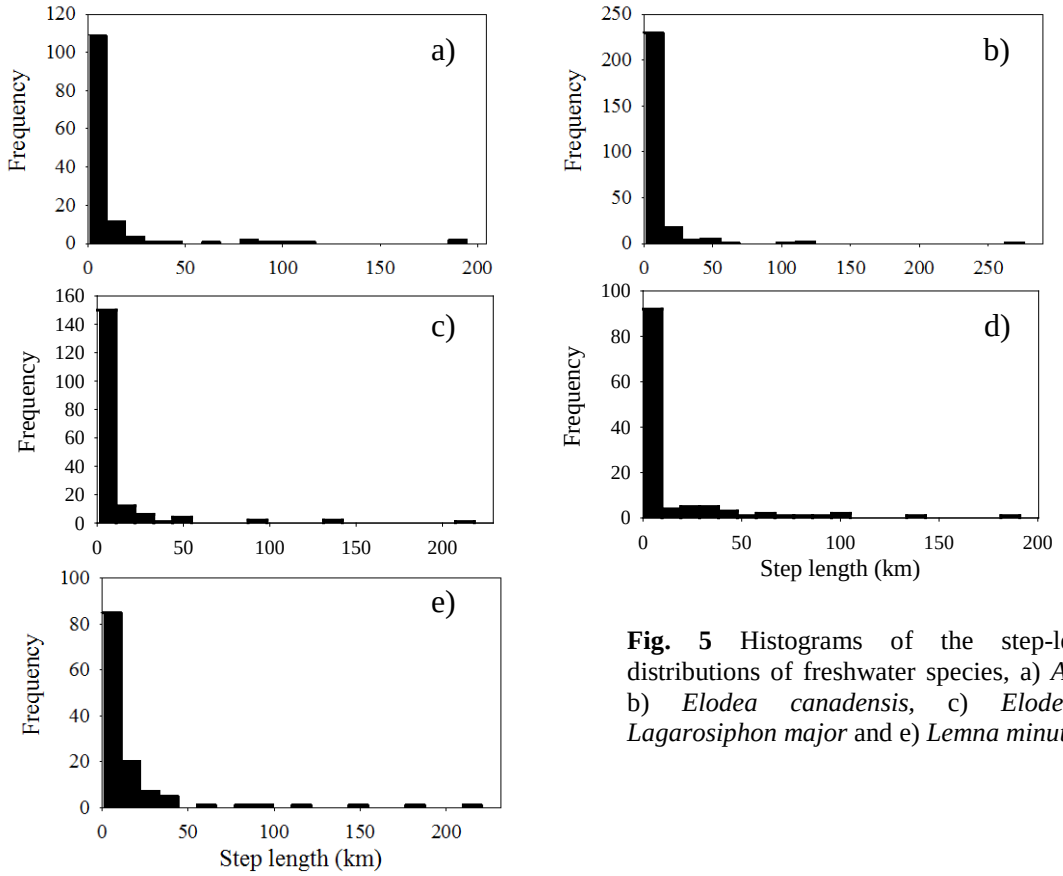

Fig. 5 Histograms of the step-length frequency distributions of freshwater species, a) *Azolla filiculoides*, b) *Elodea canadensis*, c) *Elodea nuttallii*, d) *Lagarosiphon major* and e) *Lemna minuta*.

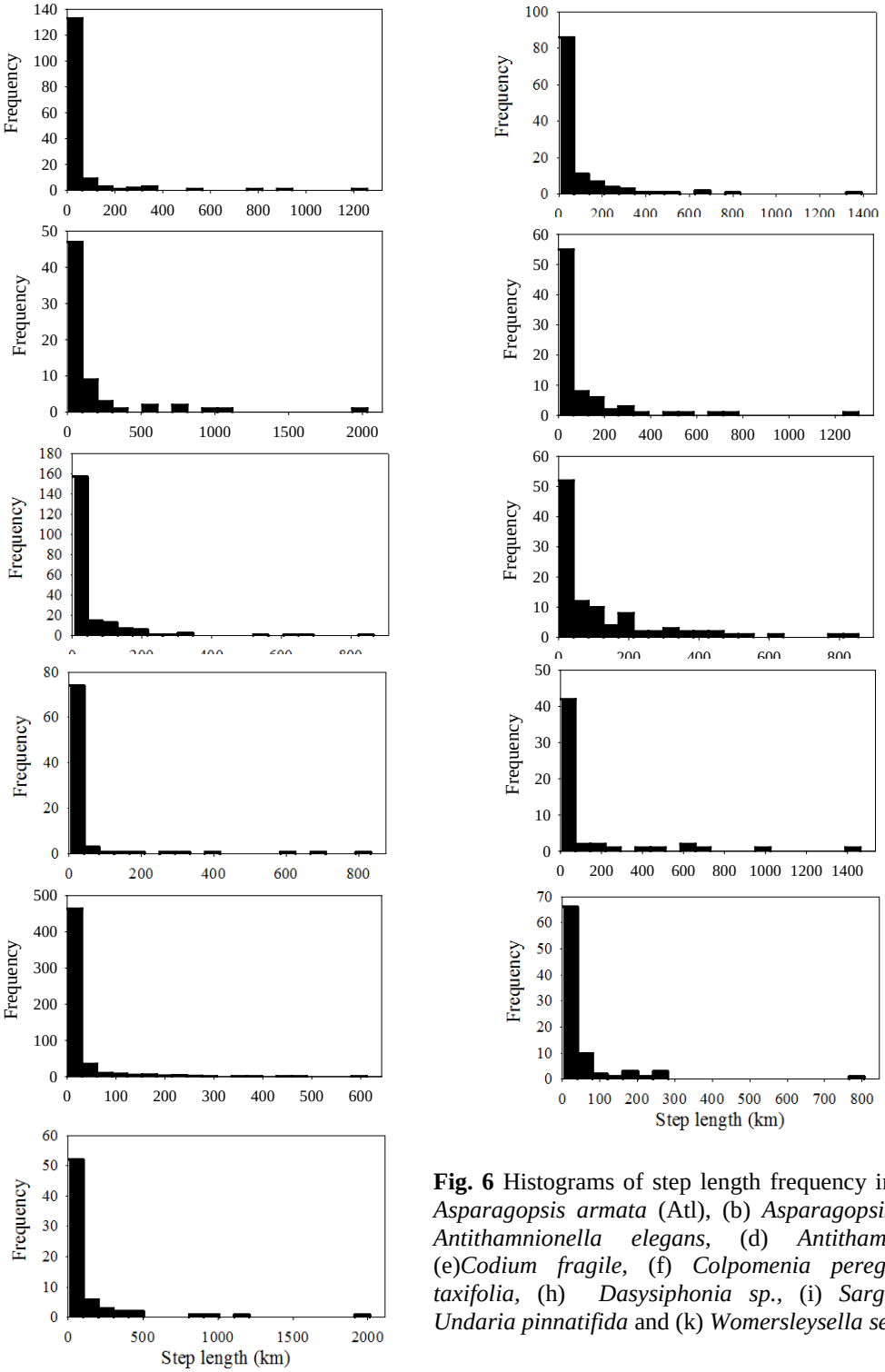

Fig. 6 Histograms of step length frequency in marine species. **(**a) *Asparagopsis armata* (Atl), (b) *Asparagopsis armata* (Med), (c) *Antithamnionella elegans*, (d) *Antithamnionella ternifolia*, (e)*Codium fragile*, (f) *Colpomenia peregrine*, (g) *Caulerpa taxifolia*, (h) *Dasysiphonia sp.*, (i) *Sargassum muticum*, (j) *Undaria pinnatifida* and (k) *Womersleysella setacea*.

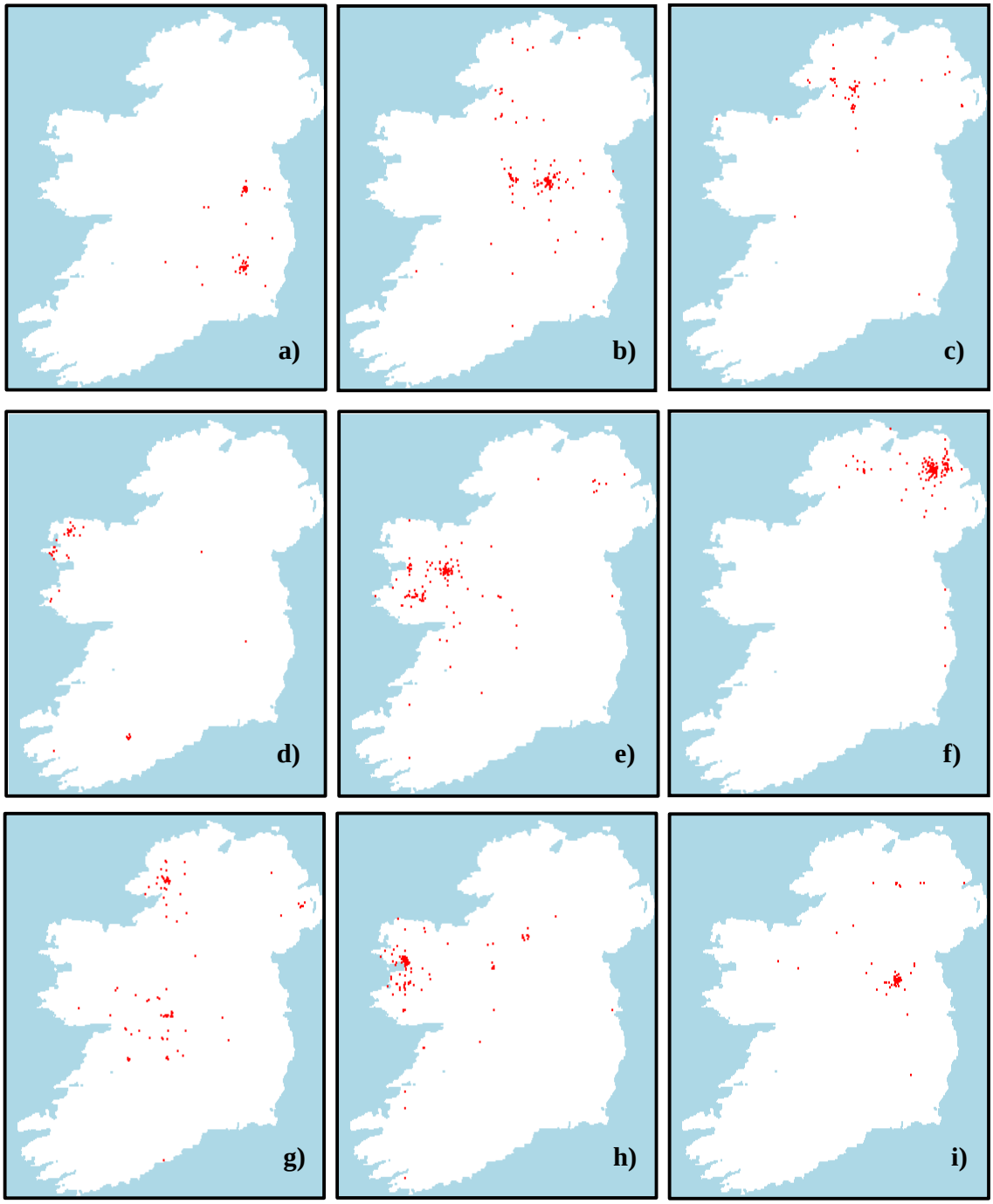

Fig. 7 Example plots of simulation model output based on power law (Lévy) dispersal. Images were selected at random from simulations, final number of points, a) 70, b) 143, c) 63, d) 55, e)175, f) 189, g) 120, h) 131 and i) 72.

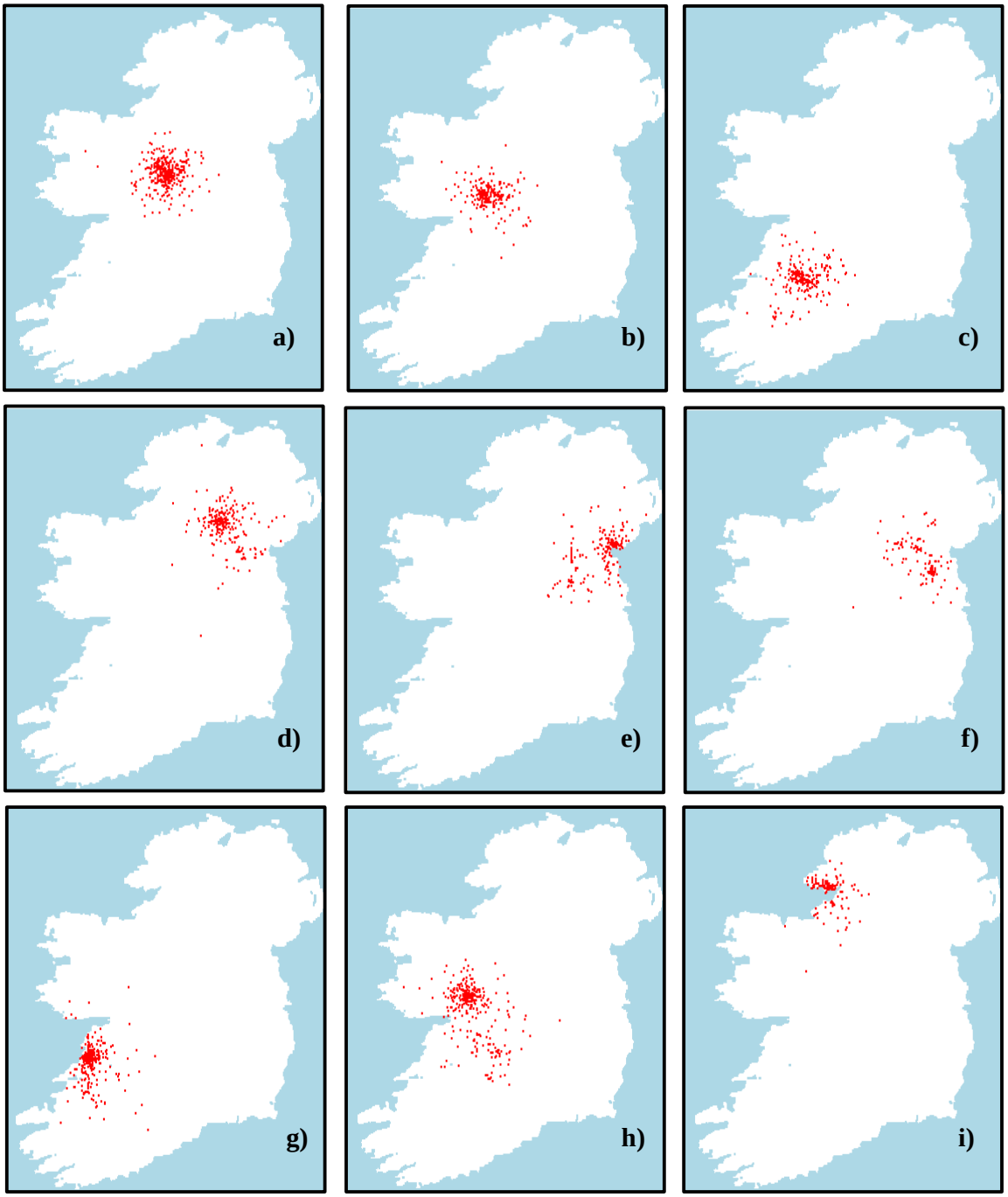

Fig. 8 Example plots of simulation model output based on exponential dispersal. Images were selected at random from simulations, final number of points (a) 419, (b) 239, (c) 229, (d) 251, (e) 227, (f) 115, (g) 316, (h) 351 and (i) 122.