Introduction

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Ecologists and conservation biologists have been aware of the problem of biological invasions for many decades (e.g. Elton 1958; Baker and Stebbins 1965). Many generalizations about invasions have been proposed, such as the notion that species-rich communities are more ‘resistant’ to invasions than their species-poor counterparts (Elton 1958; see also Levine and D’Antonio 1999; Lonsdale 1999) or that highly invasive species have certain life-history characteristics that make them good invaders (e.g. Baker 1965; Rejmánek and Richardson 1996). However, many exceptions to the proposed generalizations have been documented (see, e.g. Lonsdale 1999; Sol 2000; Chaneton et al., pp. 7–24, this issue; Simberloff et al., pp. 35–53, this issue) and our predictive ability remains limited.

One of the main obstacles to the development of a solid theory for biological invasions is our poor knowledge of the ecology of invasive species and their impacts on the recipient ecosystems. Most generalizations were proposed based on patterns observed in North America and Europe, which, given the contingent nature of ecological processes (see Lawton 1999), do not necessarily hold for other regions. Likewise, many studies of invasions focus on well-known taxa (e.g. plants, birds, mammals), but it is uncertain whether generalizations that are valid for those groups apply to other, less-studied groups. Lack of knowledge can certainly bias conclusions about invasions, as illustrated in Figure 1. There is a high, positive correlation between the number of alien plant species and the recorded number of citations on biological invasions per country. What is the explanation for this pattern? We could attribute the lower number of exotic plants in, say, Peru or Uganda, compared to Australia or Canada, to a real biological mechanism, which could in turn determine the amount of research on biological invasions conducted in each country. However, an alternative explanation is that we have not devoted the same attention to the different regions, which may in turn bias our knowledge on biological invasions. Thus, the low number of introduced plant species recorded in some countries could simply mean that we have not conducted enough research. We argue that a basic knowledge of invasions in more regions is necessary for a comprehensive understanding of biological invasions.

Improving the knowledge of biological invasions in southern South America

The southern cone of South America (i.e. Argentina, Chile and Uruguay), a region encompassing multiple climates and biomes, is not an exception to the generalized phenomenon of widespread invasion. For example, introduced species represent 12.8% of the Chilean flora, 23% of the flora of the Province of Buenos Aires, Argentina, 70% of earthworms in the Sierras Chicas in Córdoba, central Argentina, and 33% of Patagonian freshwater fish. Several other examples are given in Table 1. Clearly, invasions are occurring in many groups in many kinds of ecosystems.

Despite widespread invasion, however, not all taxonomic groups are equally represented among invaders, nor are all ecosystems equally invaded. For example, whereas 77% of Chilean aphid species are estimated to be exotic, only 0.6% of Chilean bee species are in the same category (Table 1). Likewise, although 11.5% of species of bivalves in the Río de la Plata, Argentina,
are introduced, no introduced freshwater mollusks have been recorded in Chile (Table 1).

Identifying and explaining this kind of broad taxonomic or geographic patterns is an important step towards a comprehensive understanding of biological invasions. However, such understanding requires other kinds of information on introduced species, including vectors of transportation, ports of entry, number of propagules introduced, rates of spread, and impacts on the invaded ecosystems. Relatively little effort has been devoted to improve our knowledge in these respects in southern South America. Furthermore, the available information has remained scattered in articles in a wide range of local and international journals and in the gray literature, and few attempts have been made to synthesize this knowledge. Thus, whereas in many regions there have been major syntheses on the ecology of invasions (Groves and Burdon 1986; Macdonald et al. 1986; Mooney and Drake 1986; Simberloff et al. 1997), the study of biological invasions in southern South America is still in its infancy. The contributions of this special issue are an attempt to reverse this situation.

Expanding the catalogue of invaders and their geographical distributions

Three papers included in this issue provide regional overviews of the invaders and their current regional distributions in aquatic ecosystems. Orensanz et al. (pp. 115–143) provide the first comprehensive review of invasions in coastal ecosystems of the southwestern Atlantic. They show that, contrary to what could be expected from the sparse human population, low industrialization and low agricultural development in coastal areas of this region, there have been numerous invasions. Likewise, Pascual et al. (pp. 101–113) show that ten introduced species of fish have invaded the majority of Patagonian freshwater lakes and rivers.
Table 1. Numbers of native and exotic terrestrial and freshwater species for several taxa in Argentina and Chile.

<table>
<thead>
<tr>
<th>Environment</th>
<th>Taxon</th>
<th>Region</th>
<th>Natives</th>
<th>Exotica</th>
<th>% exotic</th>
<th>Sourceb</th>
</tr>
</thead>
<tbody>
<tr>
<td>Terrestrial</td>
<td>Plants</td>
<td>Chile</td>
<td>4681</td>
<td>690</td>
<td>12.8</td>
<td>1, 2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Islas Juan Fernández, Chile</td>
<td>209</td>
<td>232</td>
<td>52.6</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Central Chile</td>
<td>2395</td>
<td>507</td>
<td>17.5</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tierra del Fuego (Arg. and Chile)</td>
<td>545</td>
<td>128</td>
<td>19.0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Buenos Aires Province (Arg.)</td>
<td>1326</td>
<td>404</td>
<td>23.4</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sierra de San Javier, Tucumán (Arg.)</td>
<td>79</td>
<td>15</td>
<td>16.0</td>
<td>6, 7</td>
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<tr>
<td>Amphibians</td>
<td></td>
<td>Pampa-Monte (Arg.)</td>
<td>83</td>
<td>0</td>
<td>0</td>
<td>8, 9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Patagonian steppe</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>8, 9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Chile</td>
<td>42</td>
<td>1</td>
<td>2.3</td>
<td>10</td>
</tr>
<tr>
<td>Reptiles</td>
<td></td>
<td>Argentina</td>
<td>–</td>
<td>1</td>
<td>–</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Chile</td>
<td>89</td>
<td>6</td>
<td>6.3</td>
<td>10</td>
</tr>
<tr>
<td>Birds</td>
<td></td>
<td>Argentina</td>
<td>951</td>
<td>11</td>
<td>1.1</td>
<td>9, 11</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Chile</td>
<td>380</td>
<td>5</td>
<td>1.3</td>
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<tr>
<td>Mammals</td>
<td></td>
<td>Argentina</td>
<td>300</td>
<td>19</td>
<td>6.0</td>
<td>9, 12</td>
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<td></td>
<td></td>
<td>Chile</td>
<td>147</td>
<td>15</td>
<td>9.3</td>
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<tr>
<td>Aphids</td>
<td></td>
<td>Chile</td>
<td>31</td>
<td>104</td>
<td>77.0</td>
<td>13</td>
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<tr>
<td>Bees</td>
<td></td>
<td>Chile</td>
<td>348</td>
<td>2</td>
<td>0.6</td>
<td>14</td>
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<tr>
<td>Oligochaetes</td>
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<td>Sierras Chicas, Córdoaba (Arg.)</td>
<td>5</td>
<td>12</td>
<td>70.6</td>
<td>15</td>
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<td>Mollusks</td>
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<td>Chile</td>
<td>132</td>
<td>9</td>
<td>6.4</td>
<td>16</td>
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<tr>
<td>Freshwater</td>
<td>Bivalves</td>
<td>Río de la Plata</td>
<td>23</td>
<td>3</td>
<td>11.5</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>Mollusks</td>
<td>Chile</td>
<td>83</td>
<td>0</td>
<td>0.0</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Fish</td>
<td>Argentine Patagonia</td>
<td>20</td>
<td>10</td>
<td>33.3</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Río Tercero, Córdoba (Arg.)</td>
<td>29</td>
<td>4</td>
<td>12.1</td>
<td>19</td>
</tr>
</tbody>
</table>

aFor marine groups, the number of cryptogenic species is also given between parentheses. bData sources: (1) Marticorena and Quezada (1985); (2) Arroyo et al. (2000); (3) Greimler et al. (this issue); (4) Rapoport and Brion (1991); (5) Söyriinky (1991); (6) Morales (1995); (7) Grau and Aragón (2000); (8) Duellman (1999); (9) Navas (1987); (10) Jaksic (1998); (11) Narosky and Yzurieta (1987); (12) Oltrog and Lucero (1980); (13) Fuentes-Contreras et al. (1997); (14) Toro (1986); (15) Mischis (1999); (16) Valdovinos-Zargès (1999); (17) Darrigran (1995); (18) Pascual et al. (this issue); (19) Haro et al. (1996). cOnly trees were included. dNo data available.

Darrigran (pp. 145–156) discusses the invasion by two bivalve species of the Paraná-Plata fluvial system, showing that they have invaded a significant portion of this large basin in a relatively short period.

These papers make evident that our knowledge of even the simplest aspects of invasions in southern South America, such as lists of introduced species and their geographical distributions, is in many cases poor. For example, only now do we have a list of invaders for marine coastal ecosystems. However, as Orensanz et al. (pp. 115–143) discuss, this list is small compared to other regions, which, as we argued above (see Figure 1), could be explained by the little research effort that there has been compared to other regions.

**Understanding the process of invasion and spread**

Several other contributions deal with different aspects of the process of invasion and spread into native ecosystems. Zalba and Villamil (pp. 55–72) analyze the invasion by woody plants in relictual grasslands in the Argentine Pampas, and Simberloff et al. (pp. 35–53) discuss the invasion by woody plants into a Nothofagus/Austrocedrus forest in the temperate forest of the southern Andes. The results of these two studies are strikingly contrasting. Whereas Zalba and Villamil found that invasion by tree species in Pampan grasslands is rampant and threatens some of the few relics of this endangered biome, Simberloff et al. found virtually no invasion in the temperate forest, in spite of high availability of propagules of over one hundred exotic tree species in plantations. Marco et al. (pp. 193–205) use cellular automata models to predict the spread of invasive species throughout the landscape, and are able to identify several important factors determining species invasiveness. The predictions of their model agree with the observed rates of spread of two exotic tree species invading montane forests in central Argentina. Greimler et al. (pp. 73–85) provide an update on plant invasions in the Juan Fernández Archipelago, where over half of the flora is composed of introduced species. The geographic distribution of
three of these species has dramatically increased during the last eighty years; they currently cover 15% of the area of the archipelago. Finally, Jaksic et al. (pp. 157–173) provide a historical account of the introduction, spread, and cross-border invasion of eight species of introduced mammals in Chilean and Argentine Patagonia. Rather than the usually assumed unidirectional spread of species, Jaksic et al. show that some invasions occur in a more complex fashion, including advances, retreats and multiple re-invasions. Their results make clear that a coordinated effort among neighboring countries may be in many circumstances necessary for the management of introduced species.

**Evaluating the impacts of invaders**

Another recurrent theme in this issue is the impacts of invaders on native ecosystems. The review presented by Orensanz et al. (pp. 115–143) shows that several species are significantly impacting most coastal ecosystems in the southwestern Atlantic. Pascual et al. (pp. 101–113) and Darrigran (pp. 145–156) point out the potential impact of introduced fish and introduced bivalves, respectively, in a large proportion of freshwater bodies in southern South America. Greimler et al. (pp. 73–85) show that three introduced plant species are modifying most vegetation types in the Juan Fernández Archipelago.

Some contributions deal with more complex interactions, such as facilitation among invaders or indirect effects of invaders on native species. Holmgren (pp. 25–33) reviews how mammalian herbivores introduced in the Chilean matorral have favored the invasion of some highly invasive shrubs, shifting the ecosystem from the original matorral to a savanna dominated by the exotic shrub *Acacia caven*. Likewise, Chaneton et al. (pp. 7–24) show that grazing by domestic cattle in the Flooding Pampas favors species richness and invasion by exotic species at local spatial scales, but reduce functional heterogeneity and diversity at the landscape level. Vázquez (pp. 175–191) shows that introduced mammalian herbivores in the temperate forest of the southern Andes are affecting many components of this ecosystem, including canopy trees, understory vegetation, and possibly native vertebrates and invertebrates. The view that different guilds of introduced species can interact positively is also addressed by Morales and Aizen (pp. 87–100); their results suggest that exotic plants common in highly disturbed areas where the forest cover has been lost may enhance the abundance of some exotic insect pollinators.

A clear pattern emerges from these studies: with few notable exceptions (e.g. the polychaete worm *Ficopomatus enigmaticus* and the barnacle *Balanus glandula* in coastal ecosystems [see Orensanz et al., pp. 115–143], or introduced herbivores in central Chile [see Holmgren, pp. 25–33]), available evidence does not allow a rigorous evaluation of the impacts of introduced species. Most accounts of impacts of introduced species are based on observational evidence or anecdotal information, and few rigorous experimental studies of these impacts have been published to date. Clearly, we need to increase our research efforts to gain a better understanding of what the myriad of species that have been recently introduced into southern South America are doing to the ecosystems they have invaded.

**What have we learned?**

The papers presented in this volume give us a very clear message: invasions are occurring in most ecosystems in southern South America, and they are spreading rapidly. We know very little about most aspects of these invasions, and if we want to reverse this situation and minimize future consequences, we desperately need to increase our research efforts. In particular, we need to expand the catalogue of invaders and obtain a more detailed picture of their geographical distributions, and to study their impacts using a combination of observational, experimental and modeling approaches. Only management and policy strategies based on sound scientific knowledge will allow us to tackle this problem adequately.

**Acknowledgements**

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References


Rapoport EH and Brion C (1991) Malezas exóticas y plantas escapadas de cultivo en el noroeste patagónico: segunda aproximación. Universidad Nacional del Comahue, Centro Regional Universitario Bariloche, S.C. de Bariloche


