Problem 5.10

If p[t+1] = (1–m) p' + m and p' = $\frac{p[t](1-s)}{p[t](1-s)+(1-p[t])}$, then the full recursion equation will equal p[t+1] = (1–m) $\frac{p[t](1-s)}{p[t](1-s)+(1-p[t])}$ + m, let's call this "recursion":

$$\textbf{recursion} = (1-m)\,\frac{p[t]\,(1-s)}{p[t]\,(1-s)+(1-p[t])}+m;$$

Part a

```
Solve[recursion == p[t], p[t]]
```

$$\left\{\{p[t]\to 1\},\ \left\{p[t]\to \frac{m}{s}\right\}\right\}$$

By hand:

$$p = (1-m)\ \frac{p\,(1-s)}{p\,(1-s)+(1-p)}+m$$

move everything to the right hand side:

$$0 = (1-m)\ \frac{p\,(1-s)}{p\,(1-s)+(1-p)}+m-p$$

put everything over a common denominator:

$$0 = (1-m)\ \frac{p\,(1-s)}{p\,(1-s)+(1-p)}+\frac{(m-p)\,(p\,(1-s)+(1-p))}{p\,(1-s)+(1-p)}$$

bring all the factors in the numerator together:

$$0 = \frac{p\,(1-s)\,(1-m)+(m-p)\,(p\,(1-s)+(1-p))}{p\,(1-s)+(1-p)}$$

$$= \frac{p-s\,p-m\,p+s\,m\,p-m\,p\,s+m+p^{\wedge}2\ s-p}{p\,(1-s)+(1-p)}$$

$$= \frac{-s\,p-m\,p\ +m+p^{\wedge}2\ s}{p\,(1-s)+(1-p)}$$

Factor the top (or use the quadratic formula to solve):

$$= \frac{(m-p\,s)\,(1-p)}{p\,(1-s)+(1-p)}$$

which equals zero if p = m/s or p = 1, the two equilibria of the system.

Part b

The polymorphic equibrium is p = m/s, which is a valid allele frequency only if it lies between 0 and 1. Given that m (migration) and s (selection against the allele "A" in the marginal population) are positive by the description of the model, p = m/s must be positive. But if will only be less than one if m/s < 1, that is, migration must be weaker than selection.

Part c

Here we need to figure out if p = 1 is a stable equilibrium. This is the code we used for the logistic:

```
derivative = D[(1 + r (1 - n[t]/K)) n[t], n[t]]
λ = derivative /. n[t] → 0
```

and here it is for this model:

```
derivative = D[recursion, p[t]]
```

$$\frac{(1-m)\,(1-s)\,s\,p[t]}{(1-p[t]+(1-s)\,p[t])^2}+\frac{(1-m)\,(1-s)}{1-p[t]+(1-s)\,p[t]}$$

```
λ = derivative /. p[t] → 1
```

$$1-m+\frac{(1-m)\,s}{1-s}$$

This can be simplified by factoring:

```
Factor[λ]
```

$$\frac{-1+m}{-1+s}$$

Comparing to the stability conditions, the equilibrium at p = 1 (allele "a" absent despite being favored in the marginal patch) will be stable if $-1 < \lambda < +1$.

In this case, $\frac{1-m}{1-s}$ will be positive because m is the fraction of migrants (can't be greater than one) and 1–s is the fitness of the "a" allele (can't be negative). So we can focus on $\lambda < 1$ (stable) or $\lambda > 1$ (unstable):

Checking when $\lambda < 1$: $\frac{1-m}{1-s} < 1$ if $1-m < 1-s$ if $s < m$ [migration "swamps" selection]

Thus, if $s < m$ then p = 1 will be a stable equilibrium, and allele "a" will fail to spread, even though it is favored in the marginal habitat.

Conversely, if $s > m$ then p = 1 will be an unstable equilibrium and allele "a" can spread when rare. [migration "swamps" selection]

Problem 5.13

If unoccupied sites (fraction 1–p) are recolonized at rate m p, which rises with the fraction of occupied patches, and if occupied sites go extinct at rate e, the following differential equation in continuous time might describe the fraction of occupied sites over time, p:

```
differential = m p (1 - p) - e p;
```

Part a

```
Solve[differential == 0, p]
```

$$\left\{\{p\to 0\},\left\{p\to \frac{-e+m}{m}\right\}\right\}$$

By hand:

$$0 = m\,p\,(1-p) - e\,p$$

factor:

```
0 = p (m (1 - p)  - e)
```

which equals zero if p = 0 or p = $\frac{m-e}{m}$, the two equilibria of the system.

- **Part b**

The equibrium with species present is p = $\frac{m-e}{m}$, which gives a valid frequency of occupied sites only if p lies between 0 and 1. Given that m (migration) is positive, p will be positive if m > e. To ensure that p is less than one requires: $\frac{m-e}{m} < 1$, that is $m - e < m$, that is $0 < e$, which is always true given extinction in the system.

- **Part c**

Here we need to figure out if p = $\frac{m-e}{m}$ is a stable equilibrium. We use the same procedure as above (we just have different rules for interpreting the derivative):

```
derivative = D[differential, p]
```

```
-e + m (1 - p) - m p
```

$$\mathbf{r = derivative\ /.\ p \to \frac{m-e}{m}}$$

$$-m + m\left(1 - \frac{-e+m}{m}\right)$$

This can be simplified by factoring:

```
Factor[r]
```

```
e - m
```

Comparing to the stability conditions for a continuous time model, the equilibrium at p = $\frac{m-e}{m}$ (species present) will be stable if r < 0, which requires that m > e.

Thus, as long as recolonization occurs at a higher rate than extinction, the species can persist and reach this dynamic equilibrium at p = $\frac{m-e}{m}$.